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Systematics and Evolution of the Andean Lizard Genus Pholidobolus (Sauria: Teiidae)

By

Richard R. Montanucci

UNIVERSITY OF KANSAS
LAWRENCE 1973

May 14, 1973

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University of Kansas
Museum of Natural History

Miscellaneous Publication No. 59

May 14, 1973

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By

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University of Kansas
Lawrence
1973

University of Kansas Publications, Museum of Natural History

Editor: Linda Trueb
Managing Editor: William E. Duellman

Miscellaneous Publication No. 59
pp. 1-52; 8 figures; 1 plate
Published May 14, 1973

Museum of Natural History
University of Kansas
Lawrence, Kansas 66044
U.S.A.

Printed By
University of Kansas Printing Service
Lawrence, Kansas

CONTENTS

INTRODUCTION 4

Acknowledgments 5

Materials and Methods 6

SYSTEMATICS 10

DELIMITATION OF SPECIES 10

GEOGRAPHIC VARIATION 16

REPRODUCTION AND BEHAVIOR 19

DISTRIBUTION AND ECOLOGY 20

EVOLUTIONARY DIVERSIFICATION IN *PHOLIDOBOLUS* 24

ACCOUNTS OF SPECIES 31

Pholidobolus Peters, 1862 31

KEY TO THE SPECIES OF *PHOLIDOBOLUS* 31

Pholidobolus affinis (Peters) 31

Pholidobolus prefrontalis new species 33

Pholidobolus montium (Peters) 34

Pholidobolus macbrydei new species 35

Pholidobolus annectens (Parker) 37

SUMMARY 38

RESUMEN 39

APPENDIX A: SUMMARY OF STATISTICS 42

APPENDIX B: SPECIMENS EXAMINED 50

LITERATURE CITED 52

INTRODUCTION

Currently about 28 genera of small teiid lizards in Central and South America are referred to the informal category of "microteiids." *Pholidobolus* is a genus of small, skink-like lizards which are less than 190 mm in total length. These lizards are characterized by relatively short, well-developed limbs, imbricate dorsal and ventral scales, and a color pattern composed of various shades of brown and cream longitudinal stripes. Populations of *Pholidobolus* are presently known only from the Andes and interandean valleys in Ecuador, occurring principally between elevations of 1800 and 4000 m. These lizards occupy a variety of habitats including semiarid grassland characteristic of the intermontane basins, montane forest on slopes and wet páramo above timber line. Differences in color pattern and morphology prevail between allopatric and parapatric populations.

The current status of microteiid taxonomy is chaotic. Considerable confusion has resulted from the definition of genera by single "key" characters, or combinations thereof. Furthermore, some "generic" characters, fundamental to microteiid taxonomy, are clearly convergent and parallel in their evolutionary history. Consequently, natural groups have been split on the one hand, whereas artificial, polyphyletic genera have been recognized on the other. Heretofore, *Pholidobolus* has been composed of a single species, *P. montium* (Peters, 1862). However, it has become evident that with a systematic review of *Pholidobolus,* the taxonomic status of several other taxa should be reassessed. These taxa include *Aspidolaemus affinis* Peters, 1862; *Macropholidus annectens* Parker, 1930; *Macropholidus ruthveni* Noble, 1921; and *Pholidobolus anomalus* Müller, 1923.

Although *Aspidolaemus affinis* has been distinguished from *Pholidobolus montium* by the absence of femoral pores in males and the presence of prefrontal scales, I consider the taxa to be congeneric. Examination of additional material (including two new species) indicates that prefrontal scales and femoral pores are not useful generic characters in this group. The occurrence of prefrontals varies inter- and intrapopulationally. For example, among populations of a new species from central and southern Ecuador, the prefrontals occur at varying frequencies; whereas, another taxon, similar to *P. montium,* exhibits prefrontals in 99 percent of the material examined. Prefrontals are variably present or absent among individuals of some local populations of *affinis.* Contrary to reports in the literature, femoral pores are present in some males of *affinis,* totally absent in *P. montium,* and variably present or totally absent among males of some populations of one of the new species. The differences that do prevail between *Pholidobolus* and *Aspidolaemus* center principally on color pattern and relatively high scale counts, and are considered to be of specific rank only. Because *Pholidobolus* precedes *Aspidolaemus* as a subgeneric name in Peters (1862) and because it was given generic status by Boulenger (1885), I place *Aspidolaemus* in the synonymy of *Pholidobolus.*

Parker (1930) considered *Macropholidus annectens* to be morphologically intermediate between *Pholidobolus montium* and *Macropholidus ruthveni* Noble. Rather than create another monotypic genus, Parker tentatively placed *annectens* in *Macropholidus.* The characters shared by *annectens* and *ruthveni* include a clear lower eyelid disc, presence of uninterrupted rows of scales around the body, and absence of lateral body folds. *Macropholidus ruthveni* differs from *annectens* in having smooth dorsals and two medial rows of greatly enlarged, hexagonal dorsal scales that are about twice as wide as long. By

contrast, the dorsal scutellation of *annectens* is like that of *Pholidobolus montium*, showing weak keels or striations, and all being subequal in size. Furthermore, additional samples of *annectens* show that the lower eyelid disc is pigmented to varying degrees in some specimens and that the scale rows around the body may be interrupted laterally by occasional scales of reduced size. In some *Pholidobolus* the lateral granules are reduced to a single row or entirely absent. Thus, the affinities of *annectens* seem much closer to *Pholidobolus* than to *Macropholidus*. Creation of a new genus to accommodate *annectens* seems unwarranted; I therefore place it in *Pholidobolus*. Provisionally, I retain *Macropholidus ruthveni* generically distinct from *Pholidobolus* because none of the members of *Pholidobolus* approaches *ruthveni* in the nature of the medial dorsals.

A species from Cuzco, Perú, described as *Pholidobolus anomalus* (Müller, 1923) has been rediscovered by Thomas H. Fritts. I have examined the specimens of *anomalus* and concur with Fritts' conclusion that the species does not belong in *Pholidobolus*. Proper allocation of *anomalus* will be the subject of a paper now in preparation by Fritts.

Species treated in this systematic and evolutionary review include *Pholidobolus affinis*, *P. montium*, *P. annectens*, and two new species described herein. Determination of the number of species to be allocated to *Pholidobolus* is based upon a discriminant function analysis of phenetically distinct populations in sympatry, and a study of concordant variation among different character states in the populations. Intraspecific geographic variation is assessed for each species by means of Simultaneous Test Procedure (STP). This aspect of the study also includes a correlation analysis designed to demonstrate the relationships between climatic parameters, such as temperature and precipitation, and morphological variation. The morphological, ecological, and geographical data thus accrued are employed in a Quantitative Phyletic analysis in an attempt to infer the evolutionary relationships within *Pholidobolus*. Largely as an outgrowth of problems encountered in the course of this study, I attempt to describe some methodological issues involved in the use of Quantitative Phyletic analysis. And finally, I test the use of quantitative phyletics as a means of identifying species. This is accomplished through a comparison of the population clusters delimited by Quantitative Phyletic analysis with those defined by discriminant function analysis and the criterion of character concordance.

Acknowledgments

The following curators kindly lent me specimens during the course of this study: Miss Alice G. C. Grandison, British Museum (Natural History) (BMNH); Dr. Walter Hellmich, Zoologisches Sammlung München (ZSM) via Dr. Thomas M. Uzzell; Dr. M. S. Hoogmoed, Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); Dr. Alan E. Leviton, California Academy of Sciences (CAS); Mr. Hymen Marx, Field Museum of Natural History (FMNH); Dr. Charles W. Myers, American Museum of Natural History (AMNH); Dr. Günther Peters, Zoölogisches Museum Berlin (ZMB); Dr. James A. Peters, National Museum of Natural History (USNM); Mrs. Dorothy M. Smith, University of Illinois Museum of Natural History (UIMNH); Dr. Charles F. Walker, University of Michigan Museum of Zoology (UMMZ); Dr. Ernest E. Williams, Museum of Comparative Zoology (MCZ). Dr. William E. Duellman kindly permitted me to use the facilities and collections in the Museum of Natural History, University of Kansas (KU). Most of the specimens collected during my study have been deposited at this institution.

Field work in Ecuador was supported by a Doctoral Dissertation Grant from the National Science Foundation

(GB-29567). A research assistantship from NSF was provided through the University of Kansas Committee on Systematics and Evolutionary Biology during the 1971-72 academic year. This study could not have been completed without the above support.

Drs. William E. Duellman, Richard F. Johnston, Charles D. Michener and Linda Trueb provided editorial comments and suggestions which improved the quality of this work. Thanks also go to Thomas H. Fritts who willingly discussed and criticized portions of this paper. Special appreciation is extended to Dr. Arnold G. Kluge, University of Michigan Museum of Zoology, who encouraged and guided my learning of the methods of quantitative phyletics. Finally, I am grateful to Drs. Bruce MacBryde, formerly of Universidad Católica del Ecuador, Quito, and Arthur C. Echternacht, Boston University, for their companionship and help in the field.

The Sums of Squares Simultaneous Test Procedure, Discriminant Function Analysis, and Quantitative Phyletic Analysis were performed at the University of Kansas Computation Center. The Quantitative Phyletic Analysis was first performed on a preliminary data set at the University of Michigan Computation Center.

Materials and Methods

Materials.—This study is based on examination of 706 preserved specimens of *Pholidobolus*. Of these, 609 specimens were used in detailed morphological study or statistical analysis. Samples for statistical purposes were drawn from specific, restricted localities, and represent localized, presumably interbreeding, populations. In a few instances adjacent localities were pooled in order to increase sample size. The local samples used for statistical studies are listed in table 1. The locations of 46 place names mentioned in the text and tables are shown on the map of the Andean region of Ecuador (Fig. 1).

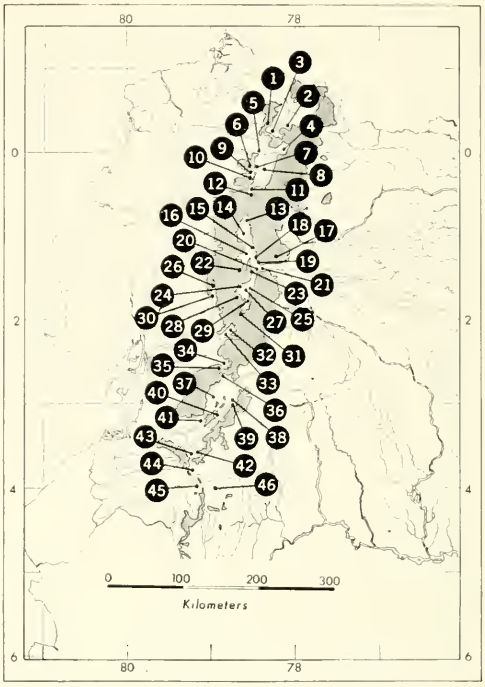

Fig. 1. Andean region of Ecuador showing the location of place names pertinent to this study. The localities are: Alausí (33), Aloag (11), Ambato (16), Baños (21), Biblián (36), Cajabamba (28), Cañar (34), Cayambe (4), Cerro Bueran (35), Cerro Llanganate (17), Cerro Pichincha (6), Chambo Grande (20), Chillogallo (10), Cotaló (23), Cubijies (25), Cuenca (37), Cumbe (40), Cutchil (39), Girón (41), Gualaceo (38), Guamote (31), Guaranda (26), Ibarra (2), Lago Cuicocha (1), Latacunga (14), Licto (29), Lloa (9), Loja (45), Los Andes (18), Machachi (12), Mulaló (13), Otavalo (3), Patate (19), Quito (7), Riobamba (27), Río Chiche (8), Saraguro (43), San Antonio (5), San José del Chimbo (30), San Juan (24), San Lucas (44), San Miguelito (15), Tixán (32), Urbina (22), Urdaneta (42), Zamora (46). Areas of 3000 m elevation and above are shaded.

Methods.—Observations on the ecology and behavior of *Pholidobolus* were made during May and June 1971. The microhabitat preferences of the lizards as well as the general vegetative and edaphic characteristics of some 30 localities were recorded. Field observations on behavior and reproduction in the lizards were made whenever possible. About 80 lizards were brought to

the laboratory for detailed observations on behavior. Color pattern variation in life was recorded from more than 300 animals.

The recognition and delimitation of species herein is based on two objective criteria: 1) geographical concordance among several independent character states; 2) sympatric occurrence (*sensu stricto*) of phenetically distinct entities, which on the basis of life history data cannot be attributed to polymorphism.

Character concordance is the coordinated distribution of several different character states through geographic space. Concordance was analyzed by plotting character states for each character on maps of Ecuador. Points of equal expression of a character were connected by lines (isophenes) which enclosed geographic regions. Areas of maximum overlap among states of different characters could be revealed by superimposing isophene distributions for all characters. Such zones of concordance (core areas) mark the codistribution of character states of different characters and serve to delimit phenetic entities to which specific names were applied. The analysis of concordance was based on nine characters (six morphological, three color pattern), chosen because of the ease of defining their character states. Independence among characters was tested by correlation analysis where possible.

Series of specimens taken from zones of sympatry were identified initially to species on the bases of head scutellation and color pattern. Although morphological intermediates were not apparent, hybrids conceivably could resemble one of the parental species in both sets of characters while favoring the other in meristic traits. To test for maintenance of integrity, Discriminant Function Analysis was applied to meristic characters only, and the results were used to corroborate the preliminary identifications. The parental species were represented by reference samples taken from areas geographically removed from the zone of sympatry. The reference localities were chosen on the basis of gross ecological and climatological similarity with the area of contact, thereby increasing the validity of comparisons among samples. A mixed sample from the zone of sympatry was treated as an unknown (test sample). Meristic characters were differentially weighted relative to their within- and between-groups variability using variance-covariance mathematics. A discriminant multiplier was calculated for each character, and this was multiplied by the value of its respective character. All such values were summed for

TABLE 1. List of local samples of *Pholidobolus* used in statistical analyses. The samples are designated alphabetically from north to south within the geographic range of each species. The abbreviation for each species is as follows: *P. affinis* (a), *annectens* (n), *macbrydei* (c), *montium* (m), *prefrontalis* (p).

Locality	Sample Size	Code
2.9 km E Pan American Hwy, nr. Mulaló	38	Aa
3 km SSW San Miguelito	6	Ba
Ambato	19	Ca
2-3 km S Los Andes	11	Da
8.9 km SSE Patate	16	Ea
Chambo Grande, 17.8 km W Baños	30	Fa
Baños	18	Ga
15 km E Riobamba	6	Ha
0.3-3.3 km S Tixán	14	Ia
Loja Valley	26	An
12 km SW Cajabamba	7	Ac
14.2 km N Biblián	23	Bc
9.1 km N Biblián	21	Cc
8-12 km S Cutchil	20	Dc
13-15 km E Loja	20	Ec
Ibarra	23	Am
Otavalo	54	Bm
Cayambe	52	Cm
4 km W San Antonio	20	Dm
San Antonio	17	Em
Quito	21	Fm
2.5 km E Río Chiche	31	Gm
2.9 km E Pan American Hwy, nr. Mulaló	8	Hm
Guaranda	31	Ap
3.3-4.9 km S Tixán	29	Bp
Alausí	16	Cp
0.5 km S Río Cañar on Pan American Hwy	9	Dp
Cutchil	12	Ep
4 km E and 6 km N Cuenca	11	Fp

each individual to yield its discriminant score. The scores of the reference samples and test sample were then plotted on frequency histograms and compared.

Sums of Squares Simultaneous Test Procedure (Power, 1970) was employed as an aid in describing major trends of variation among meristic characters within species. However, the analysis was not used to support the recognition or delimitation of species. As will be discussed later, the meristic characters in *Pholidobolus* are responsive to a complex of environmental parameters and are not very useful for diagnostic purposes. Therefore, statistical similarity between two populations need not be equated to close phylogenetic relationships.

The STP analysis employed a test of significance after an overall analysis of variance demonstrated significant differences among means. Samples were ranked in decreasing order of their means, and sums of squares were calculated by sequentially adding means (starting with the largest) until a maximal non-significant subset was delimited. The procedure was repeated, each time deleting one or more of the largest means in the previously described subset until another non-significant subset was defined, and until all samples were included in at least one such subset. A significance level of .05 was used for statistical tests. The STP tables (Tables 9-23) comprise Appendix A.

Quantitative Phyletic Analysis (Kluge and Farris, 1969; Kluge, 1969) was used to infer evolutionary relationships among the species of *Pholidobolus*. The program generates a most parsimonious dendrogram depicting the evolutionary relationships of the OTUs (Operational Taxonomic Units) in terms of cladistic events and amount of character change (patristic distance). The major strong points of the methodology include an objective technique for weighting characters according to their variability within and between OTUs, and an operational means of employing Wagner's (1961) criteria for the estimation of primitive character states.

In this study, the input OTUs were represented by the most objective units —local samples of *Pholidobolus*, that were analyzed without regard to taxonomic status. Thus, the manner in which local samples clustered and the relative patristic distances between clusters could be used in the evaluation of the species recognized by the criteria of character concordance and sympatry.

The weighting function employed in the analysis was computed by dividing the standard deviation of the sample means of the *i*th character by the average standard deviation of the *i*th character. The value obtained was then multiplied by the mean of the respective character for each sample. Characters were thus accorded weight proportional to their conservatism. Moreover, the weighting function corrects for the scaling effect shown in biological variables—the larger the structure, the greater is its variability (Kluge and Kerfoot, 1971). Averaging the standard deviation can be statistically hazardous. However, I know of no better way to obtain a weighting function based on the amount of within- and between-group variability. Applying a separate character weighting in each species of *Pholidobolus* would not compensate for potential error since there is usually as much variation within a species (local populations) as between species (see Appendix A). For discussions on the concept of conservatism and its application to evolutionary taxonomy see Farris (1966) and also Fisher (1930) and Guthrie (1965).

Proponents of Quantitative Phyletic Analysis have stressed the merits of the methodology but have almost totally neglected its shortcomings. By enumerating certain problems I hope not to discourage prospective users, but rather to instill caution and direct their efforts toward improving the methods.

When working with taxonomic categories above the species level, it is possi-

ble for a given character to be conservative in one group of organisms, yet rather variable in another. The weighting function is necessarily an average value, and to apply an average weight for the character to both groups is less than a satisfactory practice. Another problem is that cladistic results can be influenced by the relative number of low- and high-weighted characters. The low weights of several variable characters in combination may outweigh a conservative one. If considerable homoplasy is associated with the variable characters, misplacement of OTUs may occur; this can also result from the presence of correlated characters in the data set. Such characters also will unduly augment the patristic distance between OTUs. Finally, caution is urged concerning interpretation of the amount of evolutionary change depicted on the phyletic construct. Patristic distance, expressed by the relative lengths of the lines connecting OTUs, is obtained by summing the individual differences between the means of each unit character. For example, assume two OTUs, A and B, have mean values of 2.1, 2.4, 2.6, and 2.5, 2.7, 2.8 for three characters respectively. The patristic distance between A and B is 0.9, the sum of 0.4, 0.3, and 0.2. However, the difference between each pair of means may not be statistically significant; each pair of values may represent the same parametric mean. Because patristic difference is not based solely on significantly different mean values, it is possible to accrue a considerable difference between two OTUs (especially with application of a weighting function) when, in reality, a small difference, or no difference at all exists. Therefore, it is not justifiable to name a taxon on the basis of patristic distance alone.

Characters.—Specimens of *Pholidobolus* were described by a set of 21 external, meristic characters and one morphometric character. Most of the characters were utilized in the Quantitative Phyletic Analysis and Simultaneous Test Procedure. In order to minimize experimental error, only specimens in a good state of preservation were studied in detail. Correlation analyses were performed to test for redundancy among characters. Deletions of certain characters will be explained in later portions of this paper. Each character was examined for sexual dimorphism. Only femoral pores and head diameter were found to be significantly different between the sexes (females lack femoral pores and have relatively slender heads); for these characters sample means are based on males only.

Osteological comparisons (x-ray; cleared and stained specimens) were made between the species of *Pholidobolus* (N=64). Slight differences in the relative positions of cranial elements were noted among specimens, but this variation was individual in nature and does not serve to distinguish species. Characters of the axial skeleton were found to be highly conservative, defining *Pholidobolus* as a group (see Accounts of Species), but not useful at the species level. For these reasons I was unable to utilize osteological data in my evolutionary analysis of the members of *Pholidobolus*. William Presch (pers. com.) currently is comparing the osteology of the microteiids. I therefore have made no attempt to place *Pholidobolus* in any relationship to other genera. Furthermore, its apparently close relatives, *Pantodactylus* and *Prionodactylus* (Uzzell, 1969), are poorly known taxonomically; thus, an analysis of intergeneric relationships is premature at this time.

Counts were taken between structures whose homologues could be readily identified in each individual among the different samples. For example, counting the number of "occipitals" would necessarily demand the ability to distinguish these scales from "temporals." In some lizards identification would be difficult and uncertain, and counts would be subject to error. However, counting the scales in a row between the postero-

lateral edges of the orbits obviates the need for discrimination and insures high repeatability.

Definitions for each character studied are provided below:

Number of prefrontals (*NPF*).—Triangular scales (usually a pair when present) situated between the anterior corners of the ocular orbits and the posterior margin of the frontonasal plate.

Scales between orbits (*SBO*).—Scales along a straight line between the posterolateral corners of the ocular orbits.

Number of supraoculars (*NSO*).—Scales between the posterior and anterior margins of both orbits.

Number of scales along margin of upper jaw (*SUJ*).—Scales between the anterior edge of the external auditory meatus and the anterior-most extreme of the snout on one side only.

Number of scales along margin of lower jaw (*SLJ*).—Scales between the anterior edge of the external auditory meatus and the anterior-most extreme of the lower jaw on one side only.

Number of gular and jaw scales (*SGJ*).—Scales along a straight line from the collar fold (well developed fold immediately anterior to shoulders) to the anterior-most extreme of the lower jaw.

Number of ventrals (*SGV*).—Scales along a straight line from a point medial and just posterior to collar fold to the anterior margin of the vent.

Number of dorsals (*DEL*).—Scales in a straight line from the anterodorsal edge of the external auditory meatus to a point immediately posterior to the insertion of the hindlimb.

Number of temporals (*NTS*).—Scales along a straight line between the posterior corner of the orbit and the anterior edge of the external auditory meatus.

Number of scales around the body (*SAB*).—Scales around the body at a point 13 scale rows posterior to the collar fold.

Number of scales around the tail (*SAT*).—Scales around the tail at a point 9 scale rows posterior to the vent.

Number of scales along the forelimb (*SAF*).—Scales dorsally along a line between the insertion of the limb and the tip of the fourth digit.

Number of supradigital scales on fingers.—Scales along the dorsal surface of the third finger (SF3) and fifth finger (SF5) from their insertions on the palm of the hand to the tips of the digits.

Number of supradigital scales on toes.—Scales along the dorsal surface of the third toe (ST3), fourth toe (ST4), and fifth toe (ST5) from their insertions on the sole of the foot to the tips of the digits.

Number of femoral pores (*FP*).—Number of scales bearing femoral pores on both thighs and expressed as a total.

Lateral granules (*LG*).—Granular scales separating ventrals from the enlarged dorsals at a point at the 13th ventral scale row (coded 1); enlarged dorsal scales in contact with ventrals at that point (coded 0).

Lower eyelid (*LEL*).—Lower eyelid transparent (coded 0) or pigmented (coded 1).

Lower eyelid scales (*LES*).—Number of distinctly enlarged scales covering the right lower eyelid.

Head width (*HW*).—Widest point of the head (measured with dial calipers and recorded to an accuracy of 0.1 mm); the value is expressed as a proportion of the snout-vent length.

Snout-vent length (*SVL*).—Distance between the anterior-most extreme of the lower jaw and the vent; measured with a metric rule to an accuracy of 1 mm; used only to express the head width character.

SYSTEMATICS

DELIMITATION OF SPECIES

I have applied the criteria of concordance among independent character states and sympatry (*sensu stricto*) of phenetically distinct populations in the recognition of species of *Pholidobolus*.

Character concordance is the coordinated distribution of character states of several different characters through geographic space. These areas of maximum character overlap or core areas (see Methods) correspond to phenetic species (*sensu* Sokal and Crovello, 1970). As explicitly shown by Sokal and Crovello (1970), the biological species concept defined by Mayr (1963) is non-operational. I have made no attempt to define species of *Pholidobolus* on the basis of their interbreeding properties; my inferences regarding reproductive isolation apply only to the local populations investigated. However, the analysis of zones of contact and sympatry has facilitated the delimitation of the species by providing data on the existence of phenetic gaps or sharp phenetic transitions.

Character Concordance.—Nine characters and their respective states used in studying geographical concordance are: A) lateral body pattern—a. striped, b. ocellar, c. uniform; B) dorsolateral pale stripe—a. reaches snout, b. does not reach snout; C) lateral neck and tail stripes on males—a. both brown, b. both red, c. former brown, latter absent, d. both absent; D) number of supraoculars —a. two, b. three; E) number of prefrontals—a. absent, b. always present (ca. 100%), c. usually present (ca. 75%); F) femoral pores of males—a. absent, b. rarely present (ca. $< 26\%$), c. usually present (ca. 90%); G) texture of dorsals —a. striated-placoid, b. striated-keeled; H) lateral fold—a. present, b. absent; I) lower eyelid scales—a. three to six opaque scales, b. one clear or semi-opaque scale.

For some of the aforementioned characters, certain states have been arbitrarily defined to facilitate presentation of the data, but this action does not weaken or change the general conclusions to be drawn from the information. The distributions of individual states of the nine characters are shown in figure 2. Zones of maximum concordance (core areas) derived by superimposing the nine distributions are shown in figure 2J. Popu-

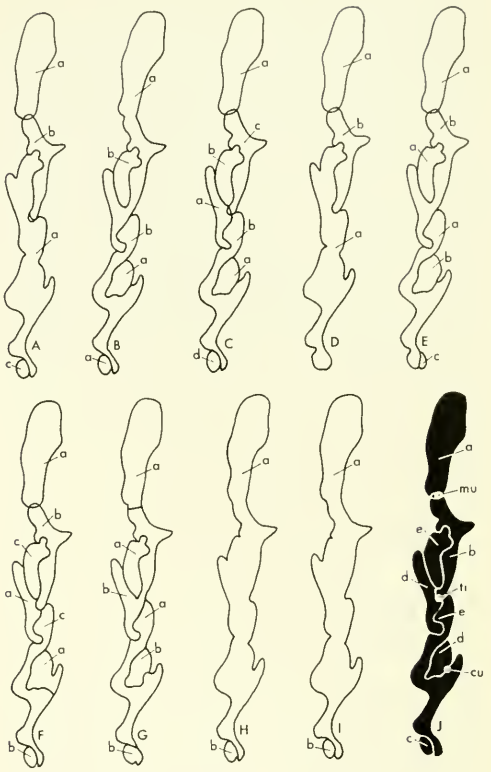

FIG. 2. The distributions of individual character states (enclosed by solid lines and designated by lower case letters) of nine characters (A-I). Zones of concordance (J) were obtained by superimposing the distributions of the nine characters. Names applicable to the core areas (J) are as follows: *P. montium* (a), *P. affinis* (b), *P. annectens* (c), *P. prefrontalis* (d), and *P. macbrydei* (e). Localities of sympatry or near contact between species of *Pholidobolus* are Mulaló (mu), Tixán (ti), and Cutchil (cu). A map like that shown in figure 1 was originally used to plot character state distributions. See text for discussion.

lations in core area (a) conform in morphologic detail to the description of *Pholidobolus montium*. Likewise, the names of *P. affinis* and *P. annectens* are available for the populations in core areas (b) and (c) respectively. Two new names, *Pholidobolus prefrontalis* and *P. macbrydei*, are proposed for the populations in core areas (d) and (e) respectively.

Sympatry.—Where two species of *Pholidobolus* come into contact, the zone

of overlap is extremely narrow. Sympatric associations were studied at two localities (Fig. 2J). Near Mulaló (mu, Fig. 2J), a mixed population of *P. affinis* and *montium* was found inhabiting a stone wall. The former species outnumbered the latter about five to one. The two species are apparently tolerant of each other, for mixed basking congregations were observed. On the basis of head scutellation, there was no evidence of hybridization, although individuals of *P. affinis* were noticeably darker in color than usual, thereby superficially resembling *P. montium*. The superficial similarity may be attibuted to a common set of environmental pressures acting upon the populations.

Discriminant function analysis (Fig. 3) based only on meristic characters (Table 2) substantiates the apparent lack of morphological intermediates. The population of *P. affinis* at Mulaló has converged towards the allopatric popu-

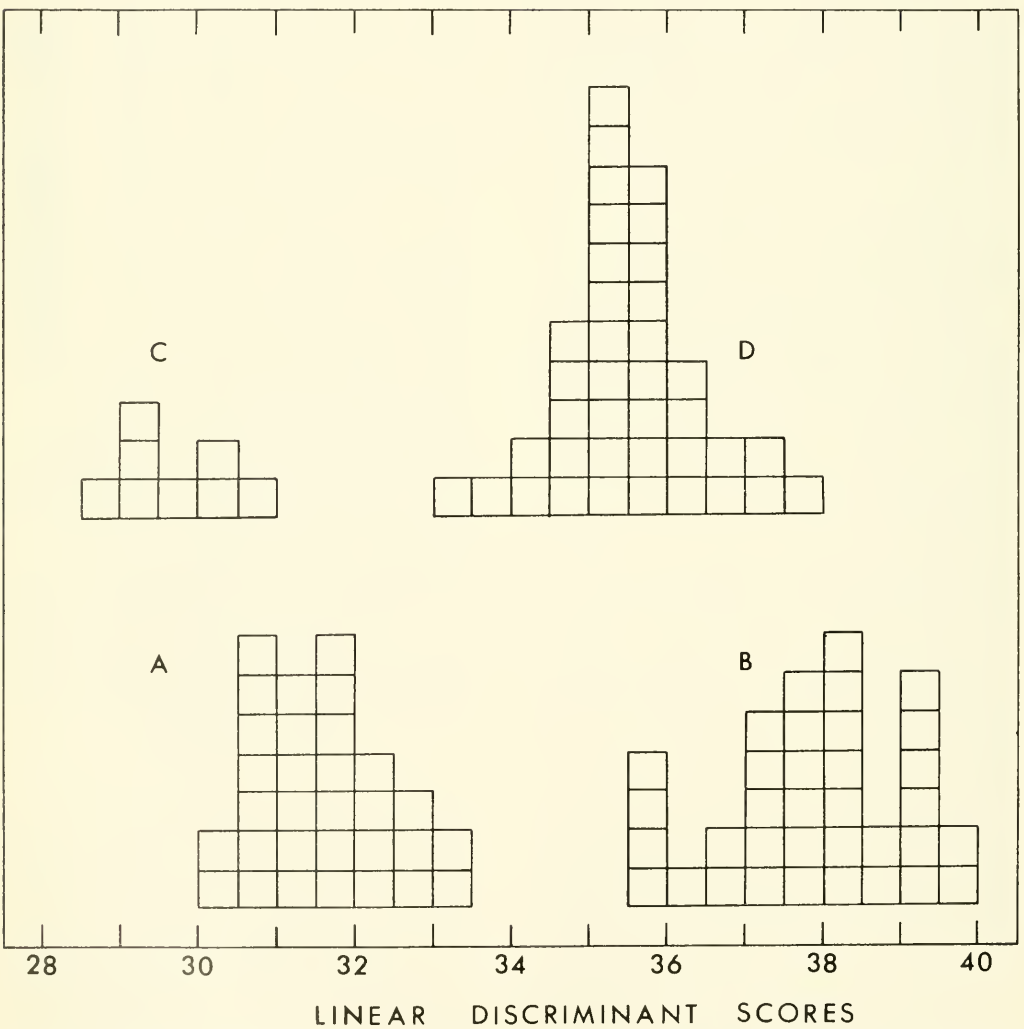

Fig. 3. Histograms of linear discriminant scores for samples of *Pholidobolus*. Allopatric reference samples are A. *P. montium* ($n = 35$, $\bar{x} = 31.5$) from the Río Chiche, and B. *P. affinis* ($n = 35$, $\bar{x} = 37.9$) from Ambato and SSE Patate. Test samples C. (*P. montium*) and D. (*P. affinis*) are from a zone of sympatry near Mulaló. Each square represents a single specimen. See text for discussion.

TABLE 2. List of meristic characters and their discriminant multipliers used in Discriminant Function Analysis comparing *Pholidobolus affinis* with *P. montium* (A) and *P. affinis* with *P. prefrontalis* (B).

Characters	Discriminant Multipliers A	B
SUJ	0.079	0.614
SLJ	0.075	−0.206
SGJ	0.083	0.454
SGV	0.282	0.222
DEL	0.146	0.162
NTS	0.485	0.345
SAB	0.025	−0.075
SAT	0.268	0.272
SAF	0.172	0.060
SF3	0.224	0.241
SF5	−0.280	0.036
ST3	0.259	0.208
ST4	0.162	0.101
ST5	−0.482	−0.365

lation (sample A) of *P. montium*. The sample of *P. montium* from the zone of sympatry seems to have undergone character displacement; its discriminant scores fall at the lower extreme of values shown for the allopatric reference sample of *P. montium*. The displacement could be attributed to competitive pressure from *P. affinis*.

On the Pacific slopes of the Andes, populations of *Pholidobolus affinis* come in contact with those of *P. prefrontalis*. The two species were found to be sympatric in a limited area about 3.3 km south of Tixán (ti, Fig. 2J). The zone of sympatry was observed briefly on two occasions. Several instances of actual or attempted homospecific copulation between lizards were seen, and adults in pairs were also noted to be conspecific. In captivity a mixed group of *P. affinis* and *P. prefrontalis* was maintained for several months. Sexual interactions observed during that time were all homospecific.

Examination of a mixed sample from the zone of sympatry did not provide evidence for hybridization on the basis of cephalic scutellation or color pattern. Discriminant function analysis based on meristic characters (Table 2) revealed two atypical specimens (Fig. 4). One of the specimens is identified as *P. prefrontalis* (KU 141103) and the other as *P. affinis* (KU 140934). The two specimens are typical of their respective species in color pattern and cephalic scutellation, and also appear normal in gross gonadal morphology. However, both specimens show extreme values for most of the meristic characters used in the analysis, suggesting that the lizards may be hybrids. If so, interspecific matings are probably relatively infrequent, chance events, because only two lizards in a series of 42 specimens show intermediate discriminant scores.

No other zones of contact were found between species of *Pholidobolus*. However, on the east side of the Cuenca Valley south of Cutchil (cu, Fig. 2J), populations of *P. prefrontalis* and *macbrydei* occur within 2 km (airline distance) of each other, and are separated by a vertical distance of only 320 m. Sympatric association may be revealed by additional intensive searching. The adjacent populations show no evidence of hybridization and the hiatus between them is sufficiently narrow to indicate that they are distinct species.

Interspecific Comparisons.—Among the characters most useful in distinguishing species of *Pholidobolus* are those associated with color pattern, cephalic scutellation and dimensions, number of femoral pores, number and condition of the lower eyelid scales, and presence or absence of lateral body folds. Diagnoses of the species are deferred for a later section of this paper. However, a summary of the morphological information is provided in table 3. Meristic characters describing body and limb scutellation are not diagnostic because of the considerable overlap among the species in the ranges of variation. Statistical differences do exist among some interspecific and intraspecific local samples. Specific comparisons can be made in only a very general sense. Most samples of *Pholidobolus affinis* show relatively high mean values compared to those of the other four species. Samples of *P.*

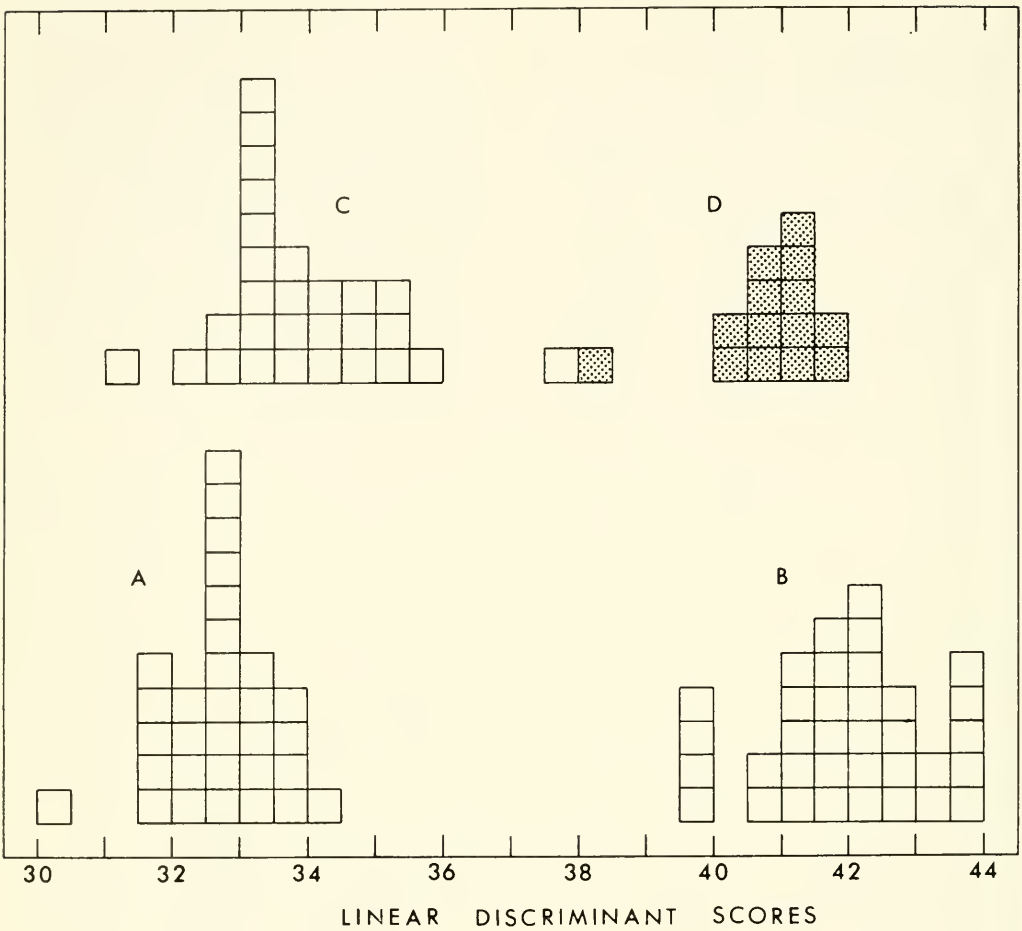

FIG. 4. Histograms of linear discriminant scores for samples of *Pholidobolus*. Allopatric reference samples are A. *P. prefrontalis* ($n = 31$, $\bar{x} = 32.6$) from Guaranda, and B. *P. affinis* ($n = 35$, $\bar{x} = 41.9$) from Ambato and SSE Patate. Test samples C. (*P. prefrontalis*) and D. (*P. affinis*, stippled) are from a zone of sympatry near Tixán. Each square represents a single specimen. See text for discussion.

macbrydei and *P. annectens* have relatively low mean values, and samples of *P. montium* and *P. prefrontalis* have sample means usually falling between the high and low extremes of most meristic characters (see Appendix A).

Note that the information in table 3 consists of the range of variation for a given character and the range for the sample means. A mean for each species was not calculated (except for *P. annectens*) because it is of no value for comparing local samples. The intraspecific local samples are sufficiently different from each other that the value of a mean of a species would be directly dependent on the relative proportion of individuals representing low and high sample means. Since the localized sample is an objective unit within which individuals are taken at random, the sample mean is most useful for comparative purposes.

Cephalic scutellation is helpful in identifying species of *Pholidobolus;* however atypical, individual variation not associated with geographical trends, occasionally occurs. The usual number of supraoculars in *P. affinis* is six (three on each side); four supraoculars are typically present in the other species.

TABLE 3. Comparison of morphological characters among the species of *Pholidobolus*. Range of variation and range of sample means (in parenthesis) are provided for each character.

Character	*P. affinis*	*P. montium*	*P. prefrontalis*	*P. machrydei*	*P. annectens*
NPF	0-3	0	0-3	0-3	0
	(1.9-2.1)	(0.0)	(1.3-2.2)	(0.0-1.5)	(0.0)
SBO	4	2-4	2-5	3-4	4
	(4.0)	(3.9-4.0)	(3.5-4.0)	(3.6-4.0)	(4.0)
NSO	5-8	4-6	4-5	4-6	4
	(5.9-7.0)	(4.0-4.2)	(4.0-4.1)	(4.0-4.5)	(4.0)
SUJ	11-15	10-14	9-14	9-13	11-12
	(12.4-13.6)	(11.0-12.4)	(9.9-12.1)	(10.7-12.1)	(11.6)
SLJ	11-15	9-14	10-13	9-15	10-13
	(12.2-13.5)	(10.4-12.2)	(11.0-11.8)	(10.4-11.9)	(10.8)
SGJ	16-26	15-22	15-20	13-22	15-20
	(19.3-22.5)	(17.4-19.4)	(16.1-18.8)	(15.6-18.8)	(17.7)
SGV	27-35	24-31	24-32	22-28	25-30
	(29.3-32.1)	(26.6-28.4)	(26.8-30.1)	(24.8-25.9)	(27.3)
DEL	45-55	35-50	37-46	31-43	40-48
	(47.4-52.5)	(40.7-46.2)	(39.5-45.3)	(40.7-46.2)	(42.6)
NTS	5-10	4-8	5-9	4-8	5-8
	(6.3-8.3)	(5.3-6.6)	(5.3-7.1)	(4.8-6.2)	(6.5)
SAB	34-54	31-45	31-45	27-41	23-29
	(38.2-50.0)	(35.0-42.1)	(36.5-40.4)	(30.3-37.0)	(26.5)
SAT	22-34	19-27	18-28	18-26	17-23
	(24.7-30.5)	(20.5-24.6)	(19.9-24.3)	(20.6-22.0)	(19.1)
SAF	22-29	18-27	20-26	18-25	20-25
	(24.0-27.1)	(21.8-24.6)	(21.3-24.1)	(19.6-23.1)	(22.4)
SF3	9-12	7-10	8-11	7-10	8-10
	(9.8-10.8)	(8.3-9.2)	(8.1-9.8)	(8.0-8.5)	(8.1)
SF5	5-8	5-8	5-7	5-7	5-7
	(6.4-7.1)	(6.0-6.4)	(5.5-6.7)	(5.5-6.3)	(6.0)
ST3	10-14	8-13	8-12	7-11	8-12
	(11.1-12.3)	(9.9-10.8)	(9.5-10.6)	(8.7-9.7)	(10.0)
ST4	12-17	10-16	10-15	9-14	11-15
	(13.9-15.4)	(12.2-13.2)	(11.9-13.6)	(10.6-12.4)	(12.2)
ST5	8-13	8-12	8-10	6-11	7-10
	(9.3-11.1)	(8.8-9.8)	(8.2-9.3)	(7.9-8.8)	(8.3)
LES	3-6	3-6	3-6	3-6	1-2
	(3.3-4.1)	(3.8-4.4)	(3.6-4.4)	(3.6-4.4)	(1.0)
LEL	1	1	1	1	0-1
	(1.0)	(1.0)	(1.0)	(1.0)	(0.1)
LG	0-1	0-1	0-1	0-1	0
	(0.5)	(0.3-0.5)	(0.4-0.5)	(0.1-0.5)	(0.0)
HW	0.151-0.180	0.155-0.175	0.150-0.177	0.164-0.204	0.154-0.166
	(0.157-0.167)	(0.159-0.168)	(0.158-0.168)	(0.168-0.195)	(0.161)
FP	0-4	0	0	0-11	0-2
	(0.0-0.5)	(0.0)	(0.0)	(0.0-10.3)	(0.4)

Some individuals of *P. affinis* taken near Los Andes, Patate, Chambo Grande, and Tixán, however, have as many as eight. The increase is usually due to fragmentation of the middle, triangular supraocular into a large inner and small outer scale. A few specimens of *P. affinis* from Baños have five supraoculars (three plus two); the two scales on one side are markedly different in size. Among the other species of *Pholidobolus,* more than four supraoculars have been noted in relatively few specimens. A single individual of *P. prefrontalis* from Alausí has five scales. In *P. montium* five or six supraoculars are present in a few specimens from Otavalo, Cayambe, Quito, and Río Chiche. Some specimens of *P. machrydei* from near San Juan, Cajabamba, and Loja have five or six scales. The supernumerary supraoculars are usually small scales fragmented from the

anterior or posterior supraocular. However, in one specimen of *P. montium* from Río Chiche, a triangular scale is wedged between the anterior and posterior scales, identical to the arrangement found in *P. affinis*.

Prefrontal scales are typically present in *P. affinis* and *P. prefrontalis*, absent or present in *P. macbrydei*, and absent in *P. montium* and *P. annectens*. A few *P. affinis* from Baños and San Miguelito lack one or both prefrontals. Some individuals from Ambato and Tixán have three prefrontals; the extra one is a small, square scale lying between the two normally present. *Pholidobolus prefrontalis* shows similar variation in the prefrontal scales. A few specimens from near Guaranda have three prefrontals, and two lizards among five taken at Biblián lack prefrontals entirely.

The typical cephalic scutellation and variations in supraocular pattern among species of *Pholidobolus* are shown in figure 5.

GEOGRAPHIC VARIATION

Results of the Simultaneous Test Procedure (STP) analysis (summarized in tables 9-23 in Appendix A) provide a basis for this discussion of intraspecific geographic variation in *Pholidobolus*. Major trends are described for 15 meristic characters studied in the following number of local samples: *P. affinis* (9), *P. annectens* (1), *P. macbrydei* (5), *P. montium* (8), and *P. prefrontalis* (6). In three-fourths of the samples, the characters SGV and DEL are significantly correlated (0.05 level); characters SF3 and ST3 are also significantly correlated with each other and with all other digit counts in most samples.

Intraspecific Patterns of Variation.— Among samples of *Pholidobolus affinis* no latitudinal clinal trends are apparent. However, high mean values for most characters are present in geographically central samples, and there is a tendency for reduction in mean values among peripheral samples from the north, southwest and east. Among the nine samples, those with means in the highest third include Chambo Grande (13 characters), Ambato (11 characters) and San Miguelito (six characters). Peripheral samples with means situated in the lowest third include Baños (13 characters), Mulaló (10 characters), and Tixán (six characters). Eleven characters (SUJ, SLJ, SGJ, SGV, DEL, SAB, SAT, NTS, ST3, ST4, ST5) exhibit high mean values in two or more of the centrally located samples and low values in two or three peripheral populations. Characters SF3 and SAF, with high mean values in three central locations, show reduction in only one peripheral locality (Baños). Characters LES and SF5 with high mean values at two central locations show reduction in the outlying samples from Mulaló and Baños respectively.

In *Pholidobolus affinis* the texture of

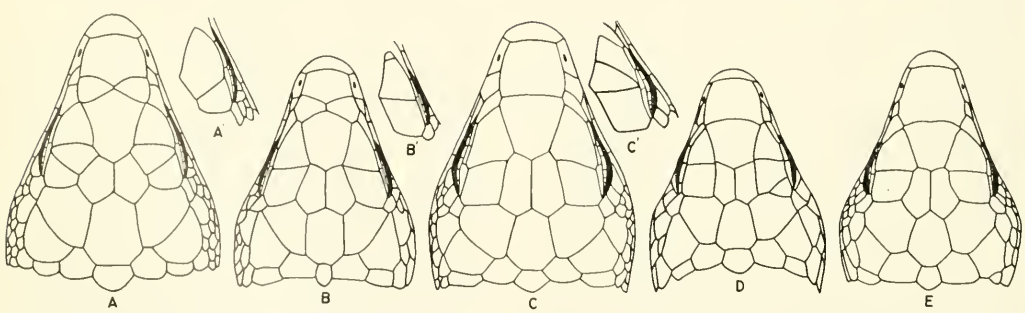

Fig. 5. Head scutellation in *Pholidobolus*. A. *P. affinis*, KU 127129; B. *P. prefrontalis*, KU 134912; C. *P. montium*, KU 118086; D. *P. macbrydei*, KU 121259; E. *P. annectens*, KU 121196. Atypical supraocular patterns are A'. *P. affinis*, FMNH 28036; B'. *P. prefrontalis*, KU 121238; C'. *P. montium*, KU 141261.

the dorsal scales varies from striated to keeled within and between local populations. The sample from Mulaló is distinctive in that nearly all individuals have smooth dorsals; weak striations are evident in a few specimens.

Four characters appear to show clinal variation in *Pholidobolus macbrydei;* however, only five samples were large enough for analysis. Mean values from smaller, geographically interspersed samples seem to support the apparent trend. Mean values of the counts show an increase from north to south with or without slight reversals. The southernmost sample from east of Loja has the highest mean values for 13 characters. Comparison of four specimens from 9.5 km south of Saraguro with the southernmost and northern samples reveals a step in the clinal patterns of two characters. In the characters SAF and SAB the sample from near Saraguro is similar to the northern samples, indicating a sharp step somewhere between the Saraguro area and the locality east of Loja. A more or less gradual clinal trend is shown by the characters ST4 and ST5.

The sample from east of Loja is also unusual in having a high frequency of prefrontal scales (ca. 75%). In other samples of *Pholidobolus macbrydei,* the prefrontals are either absent or have a low frequency. In a sample of 23 lizards from 14.2 km north of Biblián, only two individuals have prefrontal scales. Among 20 lizards from 8-12 km south of Cutchil, only one lizard was found with prefrontals.

Femoral pores are variably present or absent in local samples of *P. macbrydei.* Ranges and sample means are: four males from 10 km west of San Juan, 10-11 (10.3); ten males from 9.1 km north of Biblián, 2-11 (6.5); 15 males from 14.2 km north of Biblián, 1-11 (5.6); 11 males from east of Loja, 0-9 (3.3); five males from 12 km southwest of Cajabamba, 0-5 (2.6). Complete absence of femoral pores is known only in the sample taken from 8-12 km south of Cutchil.

Typically, the dorsal scales in *P. macbrydei* are weakly striated or placoid. The latter condition is especially evident in samples from wet páramo at high elevations. The sample from east of Loja is distinctive in having a relatively high proportion of individuals with striated or keeled dorsals. The only known specimen of *P. macbrydei* from the upper Jubones valley has keeled dorsal scales. The characters LES and SGV are statistically homogeneous among the five samples of *P. macbrydei.*

Samples of *Pholidobolus prefrontalis* show no general geographic trends, clinal or otherwise. However, for many characters, high sample means seem to be associated with xeric localities. For example, high mean values for 11 of the 15 characters (all except LES, DEL, ST5, NTS) are present in the sample from near Río Cañar which is an especially xeric locality. Means for five characters (SUJ, SLJ, SAB, SAF, LES) show relatively high values in the sample from near Tixán, which also is noticeably dry. By contrast, in the more mesic situations characteristic of the northern part of the Pacific drainage (Guaranda), the lower Andean slopes (Alausí), and the Cuenca Valley, the sample means for many characters have relatively low values. Nine characters (SLJ, SGJ, SGV, DEL, NTS, SAB, SAF, SF5, LES) have low mean values in the sample from Guaranda; eight characters show low values in the sample from near Cuenca, and seven exhibit low means in the sample from Alausí. On the east side of the Cuenca Valley at Cutchil, a population of *P. prefrontalis* shows moderate values for most characters and low values for SLJ, SUJ, NTS, and LES.

In *Pholidobolus montium* the only geographic trend evident is the presence of relatively low mean counts in samples from the northern and southern extremes of the geographical range and relatively high values in centrally located samples. At the northern end of the range, the population from near Otavalo shows low values for 11 characters (all except NTS,

SAT, SGJ, LES), and the sample from Ibarra has low mean values for SLJ, SGJ, SAB, SAT, SF3, SF5. In the southern sample from near Mulaló, seven characters show low mean values (SGJ, NTS, SAT, SUJ, SGV, DEL, SAF). Central samples, such as from San Antonio, 4 km west of San Antonio, and from near Río Chiche in the Valle de los Chillos, show high mean values for 14, 11, and seven characters respectively. These central locations are noticeably dry. Valle de los Chillos, for example, supports some species of plants known only from dry areas to the south (Bruce MacBryde, pers. com.). Therefore, an apparent association between dryness and high meristic values may apply to both *P. montium* and *P. prefrontalis*. LES is the only statistically homogeneous character in *P. montium*.

Geographic variation in *P. annectens* is not discussed herein because all localities were pooled into a single sample.

Climatic Parameters and Morphological Variation.—In the foregoing discussion I alluded to an apparent relationship between aridity and meristic variation in *Pholidobolus prefrontalis* and *P. montium*. In an attempt to understand the influence of environmental factors on character variation, simple correlation and regression analysis was applied to 20 morphological traits and two ecological parameters (rainfall and elevation) for 11 local samples of *Pholidobolus*. Correlations involving elevation were non-significant. However, inverse relationships were found between a six year average for annual precipitation and the following characters: lateral granules ($r = -0.797$, $P < .01$); scales between orbits ($r = -0.707$, $P < .05$); number of temporals ($r = -0.645$, $P < .05$); number of prefrontals ($r = -0.640$, $P < .05$). In *Pholidobolus montium* and *P. prefrontalis* a weak positive correlation was found between precipitation and the number of dorsals ($r = 0.750$, $P < .06$); lack of significance at the 0.05 level is attributed to small sample size ($N = 7$). Dorsals and femoral pores were the only characters showing positive r values among the samples. In *Pholidobolus macbrydei* an apparent reduction in number of body scales with cool-wet conditions may be adaptive. Lizards with relatively few, large body scales would have a large surface to volume ratio, enhancing solar absorption in the cool, cloudy montane environment. Furthermore, if heat loss occurs through the epidermis between scales (assuming the scales to be impermeable structures) the total area for potential heat escape is reduced by having a reduced number of body scales. The numerous, small body scales which characterize some populations of *P. affinis* and xeric-adapted *P. prefrontalis* would enable the lizard to adjust rapidly to chronic heat levels in warm-dry areas. That is to say, a small-scaled lizard once in the shade can lose heat faster than a large-scaled lizard. This hypothesis remains to be tested experimentally. For alternative models see Soulé and Kerfoot (1972). Because rainfall data were not available for localities of *P. macbrydei*, the apparent relationship between number of scales and precipitation could not be tested by regression.

Ehrlich and Raven (1969) advanced the thesis that natural selection is at one and the same time, both the primary cohesive force and the primary disruptive force producing organic diversity. They argued that the influence of gene flow between two populations depends ultimately on selection. Thus, if two populations exist under markedly different selective regimes, they will diverge despite gene flow between them. Conversely, two populations under the same or similar selective regimes will tend to remain similar even in the absence of gene exchange.

Given that climatic variables characteristic of a locality at least crudely represent the selective regime, then morphological similarity between two populations of *Pholidobolus* should proportionally reflect the climatic similarity of their localities. Regression analysis

was used to test this hypothesis. Estimates of morphological similarity based on patristic distance (amount of weighted character divergence) was taken from 15 intraspecific pairs of local samples. Several measures of environmental similarity between localities were obtained, as follow: 1) an annual rainfall index calculated by summing mean monthly rainfall differences between localities; 2) an annual temperature index calculated as above, using mean monthly temperatures; 3) a climatic index including both temperature and rainfall as calculated above. In addition, geographical distance (adjusted for topography) was calculated between pairs of localities. Patristic distance was then regressed against the variables. Non-significant correlations were obtained for geographic distance ($r = 0.064$), temperature index ($r = 0.289$) and the climatic index ($r = 0.054$). However, the correlation between patristic distance and the precipitation index was significant for a six year annual average ($r = 0.527$; $P < .05$) as well as for one year ($r = 0.528$; $P < .05$).

The influence of environmental factors on morphological variation in *Pholidobolus* is far from understood. The data indicate that precipitation is correlated with at least five meristic scale characters and can be of predictive value when analyzing overall morphological similarity between populations. Cause and effect relationships can be tested experimentally by incubating the eggs of *Pholidobolus* under different temperature and moisture regimes. Heritability studies could be used to partition variation into its environmental and genetic components. Temperature, although not correlated with meristic variation, probably interacts with other factors in a complex manner. There is no relationship between geographic distance and morphological similarity between populations of *Pholidobolus*. Thus similarity cannot be attributed to gene flow.

REPRODUCTION AND BEHAVIOR

Pholidobolus usually deposits two eggs at a time; occasionally a lizard lays a single egg on two consecutive days. Sites of egg deposition obviously are used by more than one individual, and/or repeatedly by the same individuals. Multiple clutches are known for *Pholidobolus montium*, *prefrontalis*, and *macbrydei*, and suspected for the other species. At Lago Cuicocha, one site contained 21 eggs of *P. montium*. At the bottom of a rock pile near Cutchil about 12 eggs (including old, empty shells) belonging to *P. prefrontalis* were discovered. South of Cutchil, nest sites under flat rocks contained four to six eggs of *Pholidobolus macbrydei*.

Measurements from the eggs of *Pholidobolus* (ranges followed by means in parenthesis) are as follows: 6.6-7.6 x 11.6-13.2 (7.14 x 12.38 mm) in nine eggs of *P. montium;* 6.2-9.0 x 12.0-15.5 (7.42 x 13.76 mm) in five eggs of *P. prefrontalis;* 5.7-7.4 x 10.5-12.2 (6.46 x 11.62 mm) in ten eggs of *P. macbrydei;* 6.8-7.1 x 12.3-12.8 (6.95 x 12.52 mm) in four eggs of *P. annectens;* 8.0 x 14.3-14.8 (8.0 x 14.55 mm) in two eggs of *P. affinis*.

The snout-vent length of juveniles measured shortly after hatching are: 25 mm in one *P. affinis;* 22-23 mm in two *P. annectens;* 21 mm in one *P. macbrydei;* 22-23 mm in two *P. prefrontalis*.

Females of *P. affinis* with large, yolked follicles have been collected on 11 May and 21-23 June. Individuals with oviducal eggs have been taken on 26 May and 23 June. In *P. prefrontalis*, lizards with large, yolked follicles have been collected on 11 May, 9 June, and 13 July. Females containing oviducal eggs have been taken on 12-14, 16, 24 May, 9 June, 13, 15, 25 July. Females of *P. montium* with large, yolked follicles have been collected on 26 February and 16 June. Lizards with oviducal eggs have been taken on 16 June, 17, 25 July, 31 October. In *P. macbrydei*, large, yolked follicles have been found in lizards collected on 14 May, 18-19 June, and 30 July. Lizards with oviducal eggs have

been collected on 13-14 May, 10, 19 June. In *P. annectens,* lizards with large, yolked follicles have been collected on 13 and 21 June; oviducal eggs have been noted in females taken on 12 June.

Whether the reproductive cycle in *Pholidobolus* is seasonal or continuous remains to be determined, because the above data simply reflect the field activity of collectors. Collections throughout the year are needed for each species. Telford (1971) suggested that competition between sympatric microteiid lizards in Panamá is probably reduced in juveniles by non-overlapping reproductive cycles and, perhaps, differences in diet. My data, although limited, do show that *P. affinis, montium,* and *prefrontalis* are reproductively active during the same months. Differences in diet could reduce competition between sympatric species of *Pholidobolus,* but this remains to be investigated.

Actual or attempted copulation has been observed in all species of *Pholidobolus.* The following descriptions of receptive and non-receptive behavioral patterns are typical for all members of the genus. Initially, the male crawls alongside the female, frequently licking her body. If receptive, the female remains still, permitting the male to grasp her nape with his jaws and to insert a hemipenis while his left or right hind leg straddles her lower back. If unreceptive, the female crawls continually with her body slightly raised posteriorly and her tail writhing slowly. Frequently the female stops and makes several overhand pawing motions with either forelimb. Males exhibit this same unreceptive behavior if approached sexually by other males. There is no evidence that males are aggressively territorial. In the field, males were sometimes observed in close proximity, and encounters between foraging individuals went without incident. Some microteiid lizards, for example *Euspondylus* (Fouquette, 1968), show pronounced aggressive behavior.

The mechanisms of species discrimination and mate selection in *Pholidobolus* remain to be investigated. The following evidence suggests that olfactory cues may be principally involved: 1) sympatric species of *Pholidobolus* appear to be reproductively active during the same months; 2) courtship behavioral patterns among the species are identical or at least very similar; 3) considerable licking activity occurs when members of the courting pair first encounter one another.

DISTRIBUTION AND ECOLOGY

The Andes are the dominating physical feature of Ecuador, traversing the entire country from north to south. This highland region presents a formidable barrier to east-west dispersal. The Andes consist of two cordilleras, joined in several places by east-west spurs or ridges which separate some ten intermontane basins. The Eastern Cordillera is composed principally of gneiss, mica, shist and other crystalline rocks. The Western Cordillera, however, is derived from porphyritic eruptive Mesozoic rocks and some Mesozoic sedimentary strata, chiefly Cretaceous (Sauer, 1965).

Most of the intermontane basins or valleys are situated between the Eastern and Western Cordilleras. The northernmost basins are of complex surface form, having a terrace-like peripheral rim of high terrain, and a low, inner basin excavated by river action. The Ibarra Basin, for example, shows terrace remnants between 2133 m and 2438 m; far below at an elevation of 762 m, lies the flat valley bottom along the Río Chota, a tributary of the Río Mira. Similarly, the Quito Valley shows a volcanic terrace along the lower slopes of Cerro Pichincha, ending as an abrupt scarp which drops to the floor of the basin some 2286 m above sea level. The Quito Basin is separated from the Central Valley to the south by a ridge of highlands connecting the two cordilleras. The Central Valley encompasses two basins. The northern Latacunga Basin is drained by headwaters of the Río Pastaza; the

southern Riobamba Basin also is drained by headwaters of the Río Pastaza, which flows eastward to join the Río Marañón. The Riobamba and Latacunga basins are partially separated by the massive base of Mt. Chimborazo. On the Pacific slopes, the Alausí Basin is formed along a west-flowing tributary of the Río Naranjal. To the southeast lies the Cuenca Valley, drained by headwaters of the Río Santiago, a tributary of the Río Marañón. Still farther south lie the smaller basins of Oña and Loja.

Populations of *Pholidobolus* occur throughout the Andean region. The distributions of all of the species of *Pholidobolus* are essentially allopatric or parapatric (Figs. 6 and 7). *Pholidobolus montium* occupies the northern basins of Ibarra and Quito, extending at least as far south as the northern end of the Central Valley. *Pholidobolus affinis* inhabits the Central Valley, but reaches the Pacific slopes of the Western Cordillera near Tixán. *Pholidobolus prefrontalis* occurs along the Pacific slopes from Guaranda south to Cañar and in the adjacent Cuenca Basin. *Pholidobolus macbrydei* is distributed along the crests and slopes of the Western and Eastern Cordilleras as well as on the interconnecting highland ridges. All species of *Pholidobolus* inhabit the basin floors and adjacent slopes except *P. macbrydei*, which occurs principally on the upper slopes and crests. Elevational distributions (range followed by mean) for each species are as follows: *P. affinis*, 1800-3050 (2611.1 m); *P. montium*, 2000-3190 (2726.5 m); *P. annectens*, 2150-2335 (2208.8 m), restricted to Loja Basin; *P. macbrydei*, 2315-3962 (3190.4 m); *P. prefrontalis*, 2400-2885 on Pacific slopes, and 2295-2620 in Cuenca Basin (2552.8 m).

Pholidobolus macbrydei is the most mesic-adapted member of the genus, inhabiting wet páramo grasslands and montane forests. In páramo and subpáramo situations *P. macbrydei* may be found among clumps of *Stipa*, under rocks, or in *Yucca* or bromeliads. *Pholidobolus montium* and *P. annectens* are found in similar but less mesic situations. *Pholidobolus annectens* is endemic to the Loja Basin, which has an average annual precipitation of 942.5 mm (Garcia, 1963-69). The average annual precipitation for localities inhabited by *P. montium* varies from 1039.6 to 590.2 (821.2 mm); this suggests that the species has some tolerance for dryness. *Pholidobolus prefrontalis* is primarily a xeric-adapted species. Average annual precipitation varies from 836.4 to 239.0 (481.1 mm) at localities inhabited by the species. Although *P. prefrontalis* inhabits areas that are generally drier than those occupied by *P. montium*, the tolerance limits of the two species overlap. *Pholidobolus affinis* exhibits a broad moisture tolerance, occurring in areas with an average annual precipitation of only 239 mm to as great as 1367.5 mm (634.4 mm). Thus, *P. affinis* is considered the most generalized member of the genus from the viewpoint of precipitation.

All species of *Pholidobolus* receive solar heat through basking and substrate absorption. Basking sites include rocks, agave leaves, bromeliads, or clumps of bunch grass. In the high, windswept páramo, *P. macbrydei* can be found sunning in protected situations near the bases of large bunch grasses. In subpáramo areas, the bases of *Yucca* are used for basking sites. *Pholidobolus macbrydei* remains active even after insolation has been blocked by clouds and fog. The lizards continue to receive heat through substrate absorption by pressing the body close to the surface of *Yucca* or other objects. By so doing, the lizards can remain abroad even after the ambient temperature has dropped to 18° C.

Pholidobolus usually occurs in localized, high-density populations associated with rock piles, stone walls, or agave fence rows. Distributional localization is emphasized by man's clearing of the habitat and construction of rock piles and stone walls. *Pholidobolus* may be more sparsely dispersed in undisturbed

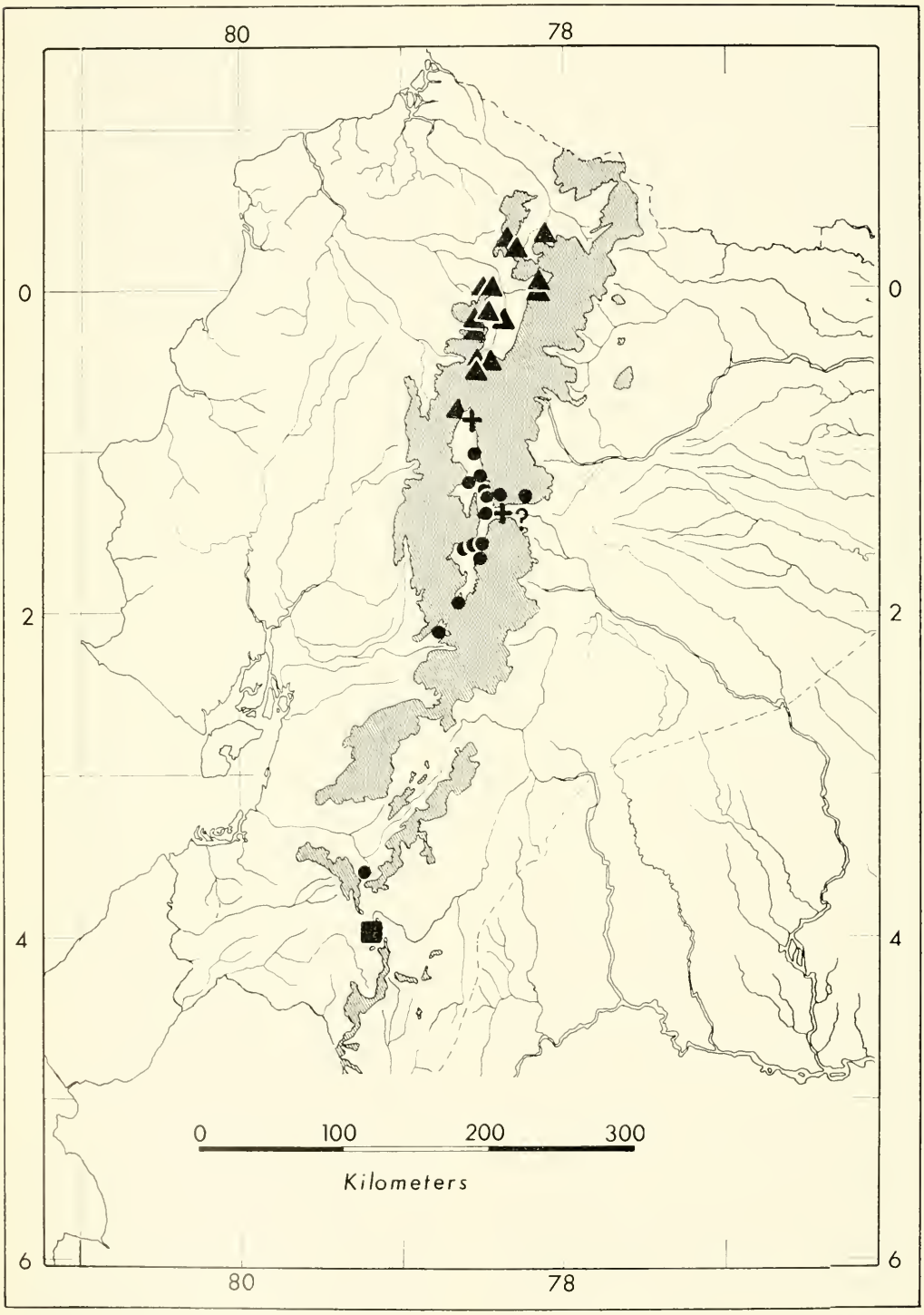

FIG. 6. Distribution of *Pholidobolus montium* (triangles), *P. affinis* (dots), and *P. annectens* (square) in the Andean region of Ecuador. Crosses mark zones of sympatry between *P. montium* and *P. affinis* at Mulaló and Baños (questionable). Areas of 3000 m elevation and above are shaded.

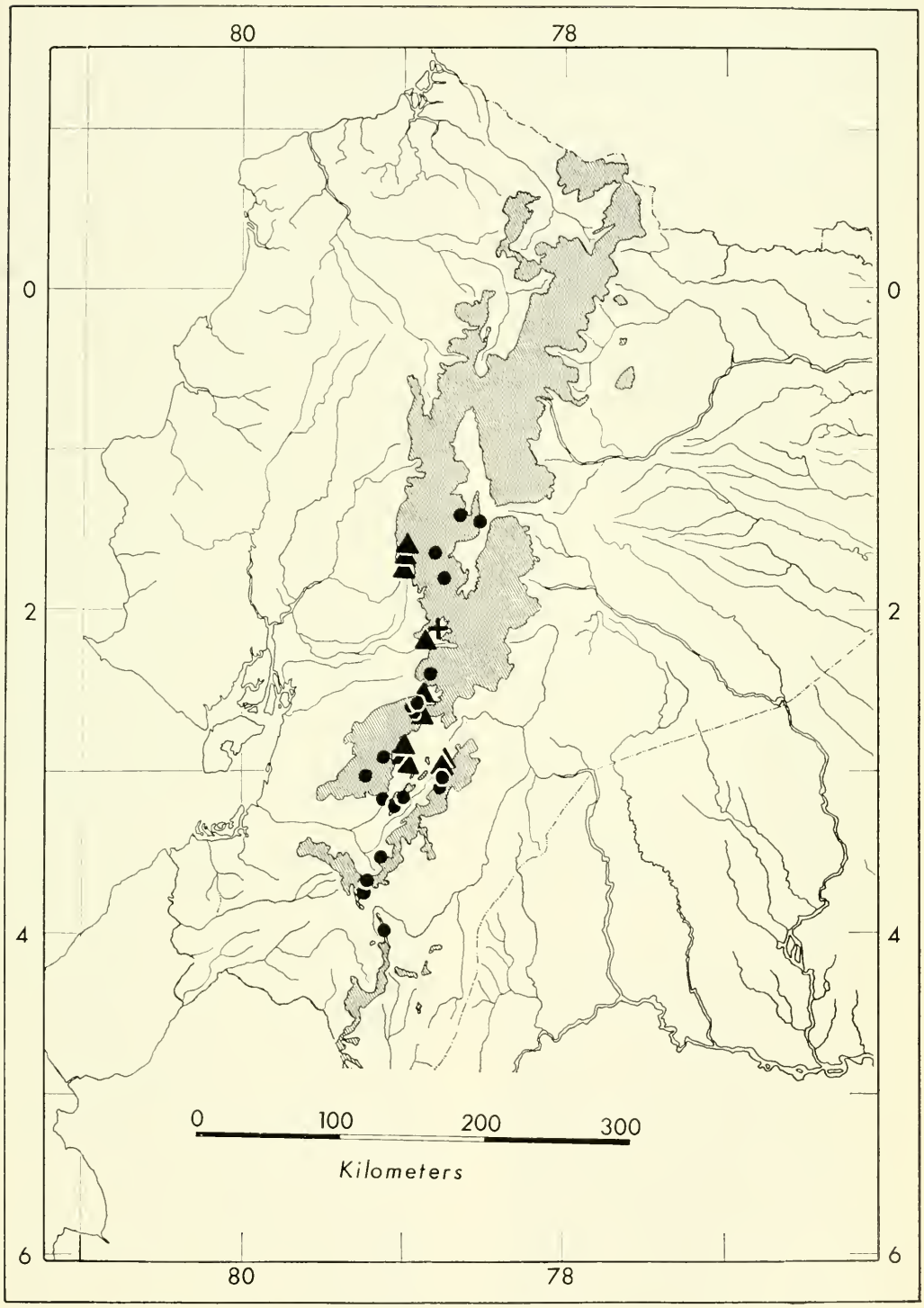

FIG. 7. Distribution of *Pholidobolus macbrydei* (dots) and *P. prefrontalis* (triangles) in the Andean region of Ecuador. Cross marks zone of sympatry between *prefrontalis* and *affinis* (see Fig. 6) near Tixán. Areas of 3000 m elevation and above are shaded.

habitat except where natural rock outcrops harbor localized, dense populations. In undisturbed, dry páramo, individuals of *Pholidobolus affinis* are relatively more scattered than those associated with stone fences. Usually a single individual is found near each clump of bunch grass or some other form of cover. In wet subpáramo habitat, single males or male-female pairs of *Pholidobolus macbrydei* are found occupying individual clumps of *Yucca* that are scattered among the bunch grass. By contrast, a dense population of *P. macbrydei* was found in a rock pile near the edge of a pasture.

Except for apparent differences in moisture tolerance, all species of *Pholidobolus* are similar in their ecology and habits. Presumably, subtle ecological differences exist between geographic areas occupied by each species, and the superiority of each species in its respective area prevents encroachment and displacement by another. Perhaps this explains why different species of *Pholidobolus* do not occur sympatrically over broad regions. By contrast, the teiid genus *Proctoporus* is sympatric with *Pholidobolus montium* and *prefrontalis* over extensive areas. Apparently the secretive habits of *Proctoporus* and perhaps other differences permit it to coexist with the free-foraging, basking *Pholidobolus*.

EVOLUTIONARY DIVERSIFICATION IN *PHOLIDOBOLUS*

Selection of Ancestral Character States.—A controversial, yet necessary, procedure in evolutionary systematics is the inference of primitive character states. Wagner (1961) recognized several criteria for estimating primitive states. According to Wagner, an ancestral state is likely to be 1) present in numerous representatives of closely related groups; 2) more widespread within a group than any one derived state, and 3) associated with states of other characters known to be primitive by other evidence. In determining the widespread nature of a character state one does not simply count numbers of taxa showing a particular state. A character state is widespread if it occurs in several taxa that otherwise have little in common. Thus, if a particular phyletic line were much more successful than others and produced many more species, etc., one would not erroneously consider a character state in that line to be primitive merely because many taxa showed that condition (Kluge and Farris, 1969).

Kluge (1969:20) employed the Prim Network as an objective method of applying Wagner's criteria. The network is an undirected, minimum length linkage system connecting OTUs on the basis of overall similarity. Wagner's criteria are founded on the premise that divergent evolution is more probable than convergent evolution in any group. Kluge (1969) reasoned that the most primitive set of character states is that OTU situated at the cladistic center of the network. This OTU directly links the most OTUs and has the smallest mean and standard deviation of interval lengths, and thus represents the point from which the largest number of different evolutionary directions can be realized.

In order to adequately estimate the "widespread" nature of a character state (criterion 2) and avoid confusing an evolutionarily successful phyletic line as a primitive one, a Prim Network analysis must include numerous "distant" taxa. Obviously use of the Prim Network has serious limitations in evolutionary studies dealing with closely related species within a single genus. The reliability of this approach to estimating primitive states increases as higher taxonomic categories are selected for study.

Teiid genera other than *Pholidobolus* could not be included in my Prim Network analysis due to paucity of material for statistical manipulations. Therefore, another approach was used to estimate ancestral states. Each character was examined separately in *Pholidobolus* and

representatives of 16 other teiid genera (actual specimens or literature descriptions). The relative primitiveness of individual character states was evaluated on the bases of ecological information and Wagner's criteria. The resulting composite suite of ancestral states was then compared with the actual OTUs of *Pholidobolus*. For purposes of discussion, I have grouped morphological characters, as follow: lower eyelid scutellation and pigmentation; lateral body folds and lateral granules; dorsal cephalic scutellation (prefrontals and supraoculars); femoral pores; body, limb, and lateral cephalic scutellation (labials, temporals). On the basis of the first and second of Wagner's criteria, the following character states are judged primitive: pigmented lower eyelid composed of several scales; presence of lateral body folds, lateral granules, prefrontal scales, three supraoculars, and femoral pores. Populations of *Pholidobolus* with low numbers of body scales are usually found in cool-wet montane habitats which are recently formed environments. Thus I consider high mean values for body, limb, and lateral cephalic scutellation to be primitive states and reduction of scutellation to be the derived condition. A composite hypothetical ancestral OTU of *Pholidobolus* therefore has the following character states: three supraoculars, two prefrontals; lateral body folds present; lateral granules present; femoral pores present; pigmented lower eyelid with several scales; relatively high mean values for body, limb and lateral cephalic scutellation. A comparison of the composite ancestral OTU with each of the species of *Pholidobolus* reveals that *P. affinis* is most primitive in its suite of character states (Table 3). *Pholidobolus prefrontalis,* although exhibiting prefrontal scales, is relatively derived in showing moderate reduction of body and limb scutellation, having two supraoculars, and totally lacking femoral pores. *Pholidobolus montium* exhibits mostly derived states—two supraoculars, total absence of prefrontals and femoral pores, and reduction in lateral granules, body and limb scutellation. *Pholidobolus macbrydei* shows the primitive condition in prefrontal scales and femoral pores among some populations, but this species is relatively more derived than ancestral in having two supraoculars, low mean values in body, limb and lateral cephalic scutellation, and reduction or absence of lateral granules. *Pholidobolus annectens* is the most derived and specialized member of the genus, having two supraoculars, a single, usually transparent lower eyelid disc, and lacking prefrontals, lateral body folds and lateral granules. The body and limb scutellation also show considerable reduction.

Ecological data support the above arrangement. *Pholidobolus montium* and *P. macbrydei* exhibit relatively narrow moisture tolerance limits and occur primarily in geologically recent habitats—montane forests and wet páramo which developed subsequent to the Andean orogeny. *Pholidobolus prefrontalis* occurs in relatively dry to xeric regions which are geologically recent, and is considered ecologically specialized. *Pholidobolus annectens,* although morphologically derived and specialized, is associated with some Amazonian floral and faunal components. However, ecological specialization is suggested by the narrow vertical distributional limits; the species does not extend below 2000 m or much above 2335 m. *Pholidobolus affinis,* by contrast, is ecologically generalized (shows a broad moisture tolerance), occurring in dry, interior basins as well as in mesic areas in the Eastern Cordillera (Baños, Cerro Llanganate), and descending to at least 1800 m. Thus, an *affinis*-like ancestor would have the greatest probability of having occupied the primitive, pre-Andean lowlands.

Although my approach to the estimation of primitive character states is subject to criticism by some evolutionary biologists, I believe my position is not only justified but preferred. The association of a particular set of characters as an integrated unit at the present time

does not mean that this set coevolved throughout all of history. The probability of this is very low for it is the change in character complexes and character state combinations that produces various levels of evolutionary diversification. Character states in a variety of combinations are obvious among groups of species and higher taxa thus providing ample evidence for potential independence of characters and/or character states at different points in evolutionary time. Thus considering characters potentially independent and treating them independently for estimation of ancestral states constitutes a minimum assumption.

In two Prim Networks generated from weighted and unweighted data sets of *Pholidobolus*, an OTU of *P. montium* represents the cladistic and patristic center in each case. For reasons presented above, I consider *P. montium* to be a relatively derived species. If my interpretation is correct, the position of the *montium* OTU on the Prim Network would indicate evolutionary success, i.e. the species *macbrydei*, *prefrontalis*, and *annectens* arose from a *montium*-like progenitor. The close relationship among these species is apparent because they are linked together on the basis of two supraoculars, absence of prefrontals (except *prefrontalis*), and generally low values for 14 meristic characters of the body and limbs (see Table 3 and Appendix A). On the other hand, *affinis* is distinct in having 3 supraoculars, 2 prefrontals, and high mean values for the meristic characters of the body and limbs. The position of a potential ancestral OTU relative to the cladistic center of a Prim Network also can be a function of the relative number of related and unrelated OTUs in the analysis. The cladistic position would become a sampling phenomenon when using local populations as input OTUs (i.e., including many local populations that are closely related to the potential ancestor would effect its central position), or would become an evolutionary phenomenon when using species or higher categories as input OTUs.

Phyletic Constructs and Character Consistencies.—A total of four Wagner Diagrams was generated from various modifications (see below) of the weighted data set of *Pholidobolus*. Orientation of the phyletic constructs was achieved by rooting with the composite ancestral OTU. In the first dendrogram generated from a limited data set, a sample of *P. macbrydei* (with prefrontal scales) clustered with *P. prefrontalis*. The misclustering was corrected by adding a morphometric character (HW). An additional problem was encountered with the incorporation of new samples. The sample of *P. prefrontalis* from near Río Cañar fell between the clusters of *P. montium* and *P. affinis*. The sample from Río Cañar exhibits high mean values for several meristic characters (see Appendix A); apparently the sum of the low weights of the characters overrode the influence of the few, high-weighted diagnostic characters. Correlation analysis revealed that characters ST3 and SF3 are highly correlated with each other and with other limb characters and thus were deleted. The character SBO also was deleted simply because of the lack of significant mean differences among samples. In addition, significant correlation was noted between SGV and DEL among the majority of samples. Proper clustering of the Río Cañar OTU was achieved by deleting either SGV or DEL. The dendrogram without SGV shows a higher consistency value than does the construct lacking DEL. Moreover, the relative weight and unit character consistency of DEL is greater than that of SGV. Therefore, the Wagner Diagram with DEL (lacking SGV) was chosen as most parsimonious (Fig. 8). The total length of the construct is 484.7, and its consistency index is 0.488 (a consistency value of 1.00 would indicate no homoplasy).

One can argue that a consistency index of 0.488 demonstrates that there is so much homoplasy present among the

Table 4. The patristic distance between the closest interspecific demes (A), and the greatest patristic distance between phyletically adjacent conspecific demes (B).

A. *P. affinis*—*P. montium* (Baños—San Antonio)	31.7
P. montium—*P. annectens* (Otavalo—Loja Valley)	42.7
P. montium—*P. prefrontalis* (Mulaló—Guaranda)	20.9
P. montium—*P. macbrydei* (Otavalo—S Cutchil)	55.6
P. prefrontalis—*P. macbrydei* (Guaranda—S Cutchil)	75.4
P. annectens—*P. macbrydei* (Loja Valley—E Loja)	85.7
B. *P. affinis* (SSE Patate—Tixán)	28.3
P. montium (W San Antonio—Cayambe)	17.9
P. prefrontalis (Guaranda—Cutchil)	31.6
P. macbrydei (E Loja—S Cutchil)	36.2

characters that the phylogenetic conclusions drawn are very questionable. I attribute the low consistency index to the use of local population samples as input OTUs. One of the characteristics of local biological populations is their capacity to differ from one another statistically. Any character, especially a meristic one, can be expected to change in mean value from one local sample to the next. Thus, on a phyletic construct, numerous character state reversals are not only possible, but likely, and when many meristic characters are taken together (as in this data set) the effect can be compounded, resulting in a relatively low consistency index for the Wagner tree. When all the local population values are averaged into a mean for each species, the number of possible character steps can be greatly reduced and with little or no effect on the observed range for the character. For example, the unit character consistency for DEL is 0.403 (Table 5) when the input OTUs are local samples. After pooling the samples to obtain a mean for each species, the consistency index for DEL was recalculated using essentially the same sequence of OTUs as in the original character state tree, but adjusting the observed range of DEL to correspond to the new mean values. The consistency index thus obtained for DEL was 0.921, indicating little homoplasy! In like manner (using species as input OTUs) the overall consistency index for the phyletic construct could be greatly increased. However, I am interested in the relative positions of the local populations from the standpoint of morphological similarity. I am not purporting to show evolutionary relationships between local populations, but only between local population clusters (species); the sequence of the clusters is significant from the standpoint of evolution. Hence, the aforementioned criticism regarding low consistency has no validity here. I consider the arrangement in figure 8 to be a reliable estimate of the evolutionary relationships between the species of *Pholidobolus*.

The local samples of *Pholidobolus* on the phyletic construct cluster according to the species recognized herein by the criteria of character concordance and sympatry. In most cases, the interspecific patristic distance is greater than the distance between intraspecific demes (Table 4). A notable exception, however, occurs in *Pholidobolus prefrontalis*. For example, the patristic distances between OTUs from Guaranda (Pacific slope) and Cutchil or NE Cuenca (Cuenca Basin) are greater than the minimum distance between *P. montium* and *P. prefrontalis*. There is no doubt that the samples from the Pacific slopes and the Cuenca Basin are conspecific. Together they form a monophyletic cluster, have in common conservative characters of head scutellation, and share other characters (keeled dorsals, color pattern), which were not used in the evolutionary analysis. The great intraspecific divergence is attributed to the cumulative difference of several low-weighted, meristic characters.

Table 5 shows the relative weight and consistency of each character. Using a nonparametric test (Spearman's co-

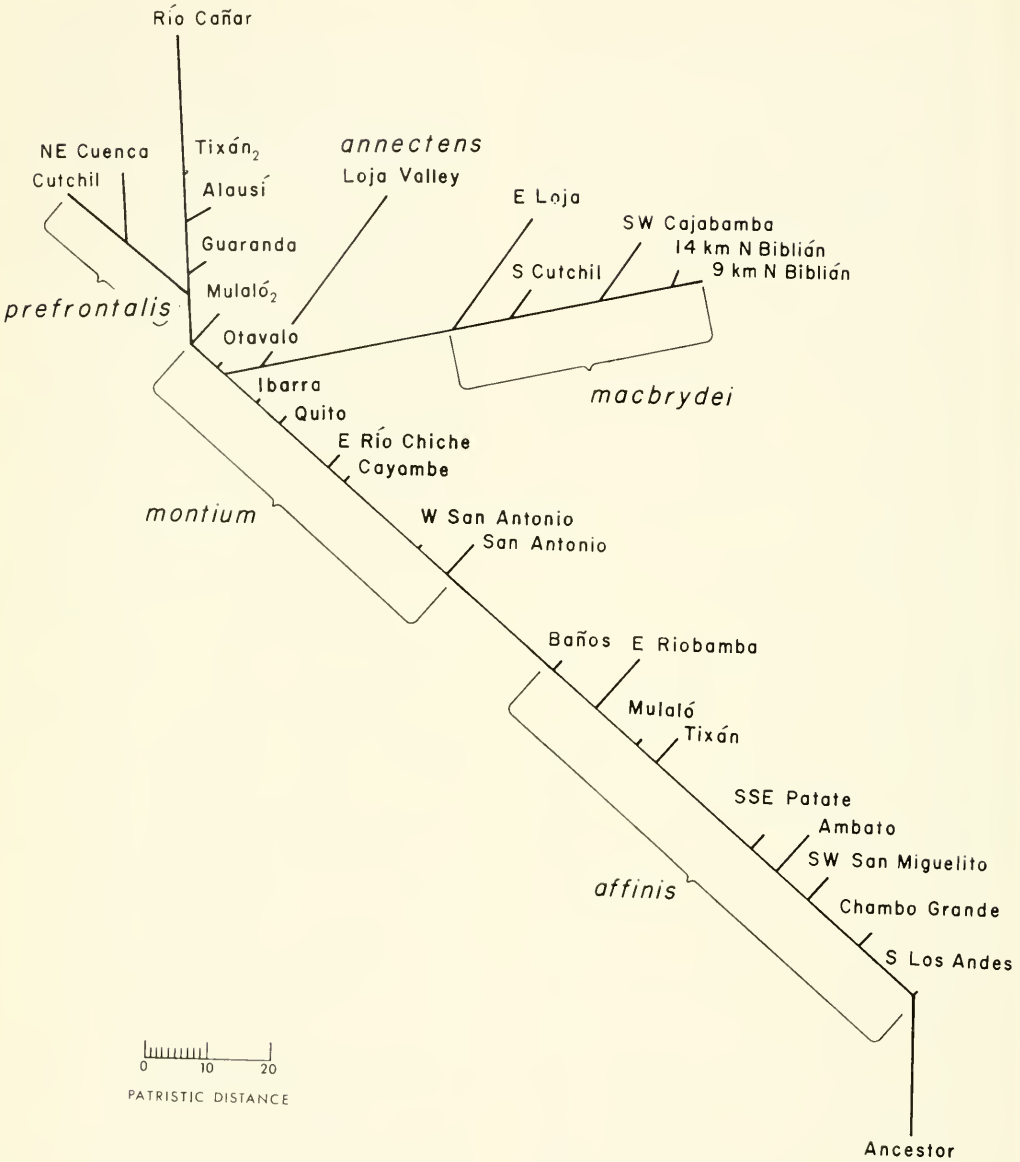

FIG. 8. A Wagner Diagram based on 29 OTUs (local samples) of *Pholidobolus*. Relationships are drawn to scale. For discussion and interpretation see text and tables 4 and 5.

efficient of rank correlation), I found no association between the *a priori* estimation of relative weight and unit character consistency. Thus there is low predictive power between the two parameters in this data set. Although characters of head scutellation (NSO, NPF) and body-tail scutellation (DEL, SAB, SAT) are more conservative than the others, considerable homoplasy is associated with the majority of characters. As explained earlier, the low character consistencies can be attributed to the meristic nature of the characters themselves and the use of local biological populations as the input OTUs. The character LEL (a binary state character) shows no homoplasy. On a probability basis,

one would expect different saurian groups to share the same or similar average numbers of scales more frequently than to share a structural specialization. The high weight but low consistency of NPF suggests that it is adaptive (or at least associated with an adaptive trait), and has been subjected to changing selection pressures relatively frequently through evolutionary time. The nature of prefrontal scales should not be used as a generic character in the taxonomy of microteiids, because the scales may be non-homologous even among individuals within a local sample. This conclusion follows from differences noted in the position of the scales relative to the anterior corner of the ocular orbit. In some specimens the scales have been formed by fragmentation of the frontal plate, but in other specimens the scales have been derived largely or entirely from the supranasal plate. Formation of the prefrontal scales has not involved changes in configuration of cranial elements. Regression of head length (ear to snout terminus) against snout length (eye to snout terminus) in samples with and without prefrontal scales resulted in a tight cluster of points with no significant differences in slope or y-intercept. Comparisons have been based on samples of *P. macbrydei* with and without prefrontal scales, *P. prefrontalis* and *P. montium*, and *P. affinis* and *P. montium*.

Evolutionary Perspective.—The relative positions of the species clusters on the Wagner Diagram (Fig. 8) indicate that an *affinis*-like ancestor gave rise to a derived, generalized *montium*-like stock; the latter, in turn, underwent evolutionary radiation producing several ecologically or morphologically specialized species. Essentially the same cladistic result is obtained from the four dendrograms generated; they differ only in the relative positions of local samples within a given species cluster. Evolutionary interpretation is most meaningful at the level of species clusters. I do not attach evolutionary significance to the sequence of local samples within a cluster. Earlier discussion revealed that morphological closeness of geographically distant demes is apparently a reflection of climatic similarities between localities. Therefore, patristic relationships between intraspecific samples are best regarded simply as measures of morphological affinity.

TABLE 5. The relative weight and consistency of each character used in the Quantitative Phyletic Analysis of *Pholidobolus*.

Character	Weight	Consistency
NPF	3.39	0.304
NSO	2.69	0.567
SUJ	1.38	0.309
SLJ	1.18	0.352
SGJ	1.83	0.318
DEL	2.42	0.403
NTS	1.31	0.286
SAB	2.46	0.411
SAT	2.29	0.470
SAF	1.94	0.398
SF5	0.96	0.408
ST4	1.50	0.412
ST5	1.23	0.340
FP	1.64	0.476
LG	0.53	0.357
LEL	0.65	1.000
LES	1.05	0.457
HW	1.18	0.780

Probably all high northern Andean biotic patterns have developed since the end of the Tertiary, and most have been explained in terms of Pleistocene climatic events (Haffer, 1970; Vuilleumier, 1971). The great influence of glacial-interglacial oscillations on plant and animal distributions has been the fundamental assumption underlying the interpretation of speciation patterns. During glacial periods, areas under permanent ice are thought to have increased. Presumably this resulted in the lowering of vegetative zones, and thereby permitted high montane organisms to disperse through suitable habitat to adjacent mountain ranges. During interglacial periods, intermontane valleys and passes became arid; thus, xeric-adapted forms were allowed to spread, whereas mesic-adapted, montane organisms were restricted or isolated. Admittedly, this in-

terpretation is simplistic. It does not take into consideration such factors as physiographic features influencing precipitation and drainage patterns, or minor climatic oscillations which must have occurred during the major glacial and interglacial periods. Therefore, the picture of climatic change, dispersal, and evolution of Andean organisms during the Pleistocene probably is more complicated than generally has been thought.

There is evidence that the distributional patterns of *Pholidobolus* were modified by climatic oscillations during the Pleistocene. The southern isolate of *Pholidobolus affinis* near Saraguro indicates that the distribution of this species was more widespread than it is at present. Perhaps during a dry climatic period, populations of the derived, xeric-adapted *Pholidobolus prefrontalis* dispersed southward along the Pacific slopes and through the Cuenca Basin, displacing the ecologically generalized *P. affinis* from most of its former range. This explanation is considered the simplest interpretation of the present distributional relationships of the two species. During one or more wet climatic periods, mesic-adapted, *montium*-like populations (progenitors of *P. macbrydei*) were able to spread southward along the Eastern and Western cordilleras. During dry periods, these populations could have survived in mesic, high slope and crest situations, especially along the Amazonian slopes of the Eastern Cordillera. *Pholidobolus annectens*, a species endemic to the southern Loja Basin, is a dispersal product of the *montium*-like progenitor populations. *Macropholidus ruthveni*, apparently a highly specialized derivative of *Pholidobolus* stock, provides evidence that the southward dispersing progenitors reached northern Perú.

Vuilleumier (1971) placed great emphasis on isolation by geographical and ecological (glacial and vegetative) barriers as the mechanism for speciation in high Andean organisms during the Pleistocene. Major evolutionary diversification of *Pholidobolus* probably occurred during this time. However, I do not consider isolation necessary in explaining speciation in *Pholidobolus*. Ehrlich and Raven (1969) provided evidence supporting their contention that natural selection is the major evolutionary force and that ultimately, it determines what effect gene flow will have between populations. In *Pholidobolus* several lines of evidence support this argument. First, there is no correlation ($r = 0.064$) between geographical distance and morphological similarity among intraspecific local samples. If gene flow were maintaining the similarity between populations, one would expect adjacent samples to be more similar to each other than to progressively distant samples. Second, maximal glacial extension depicted by Sauer (1965) would not have formed complete barriers between the interandean basins occupied by *Pholidobolus*. Montane passes apparently existed between the Quito and Latacunga basins, the Riobamba and Alausí basins, and between the Cuenca and Alausí basins. Third, the existence of vegetative barriers between incipient species of *Pholidobolus* is unlikely. The moisture tolerance limits of the species overlap in part and each species (except *P. annectens*) inhabits several vegetative associations. There is little reason to believe, for example, that the evolution of *P. macbrydei* and *P. prefrontalis* from a common stock involved ecological isolation. Ancestral populations in the dry Alausí and Cuenca basins could have diverged from populations on the adjacent, wet slopes in response to differential selection pressures while maintaining parapatry (parapatric speciation). The probable effect of glacial-interglacial oscillations simply would have been to displace vertically the zone of contact. The divergence of *P. montium* from an *affinis*-like progenitor can be argued similarly. Therefore, speciation in *Pholidobolus* can be best explained in terms of different selective regimes acting upon the populations through time.

ACCOUNTS OF SPECIES

The genus *Pholidobolus* is known only from the Ecuadorian Andes. Detailed locality data for each species are presented in appendix B. Distribution maps are shown in figures 6 and 7.

Pholidobolus Peters, 1862

Pholidobolus Peters, 1862, Abh. Akad. Wiss. Berlin, 1862:195 (Type species.—*Ecpleopus* (*Pholidobolus*) *montium* Peters, 1862, by monotypy).

Aspidolaemus Peters, 1862, Abh. Akad. Wiss. Berlin, 1862:199 (Type species.—*Ecpleopus* (*Aspidolaemus*) *affinis* Peters, 1862, by monotypy).

Diagnostic Definition.—1) Teiid lizards of Group II (Boulenger, 1885) having snout-vent lengths of 66 mm or less; 2) tail accounting for 69 percent or less of total length; 3) limbs pentadactyl, digits clawed; 4) body and tail cylindrical, neck not greatly constricted; 5) head distinctly flattened, depth 59-73 (67.7) percent of width; 6) tympanum deeply recessed; 7) snout obtusely pointed; 8) nostril piercing nasal suture; 9) dorsal scales imbricate and weakly keeled to striated with some placoid; 10) dorsal scales in transverse series; 11) dorsal scales longer than wide, quadrangular to subhexagonal; 12) gular scales smooth, imbricate, becoming larger posteriorly; 13) two medial rows of widened gulars anterior to collar fold; 14) ventral scales smooth, imbricate; 15) ventral scales rectangular, in transverse and longitudinal series; 16) tongue covered with imbricate, scale-like papillae; 17) hemipenes with minute calcareous spines; 18) 26-27 presacral vertebrae; 19) 21-23 ribs; 20) 5-6 pairs of ribs attached to pectoral girdle; 21) one pair of abdominal ribs attached to each other midventrally, posterior to the xiphisternum.

KEY TO THE SPECIES OF *PHOLIDOBOLUS*

1. Three supraoculars, middle one wedged between first and third with apex usually reaching superciliary row (Fig. 5A); two prefrontals ..... *P. affinis*
   Two supraoculars, subequal in size 2
2. Prefrontals present 3
   Prefrontals absent 4
3. Dorsolateral pale stripe distinct, extending to tip of snout; femoral pores absent in both sexes; head not distinctly broader in males than in females; sides of neck and tail without red stripe (orange-brown in preservative) in males ..... *P. prefrontalis*
   Dorsolateral pale stripe distinct, not extending to tip of snout; femoral pores usually present in males; head distinctly broader in males than in females; sides of neck and tail with red stripe in males ..... *P. macbrydei*
4. Lower eyelid usually having a single transparent disc; lateral granules usually absent at midbody; dorsum uniformly gray-brown ..... *P. annectens*
   Lower eyelid having 3-6 opaque scales; lateral granules usually present at midbody 5
5. Dorsolateral pale stripe distinct, not extending to tip of snout; femoral pores usually present in males; head distinctly broader in males than in females; sides of neck and tail with red stripe in males ..... *P. macbrydei*
   Dorsolateral pale stripe distinct, extending to tip of snout; femoral pores absent in both sexes; head not distinctly broader in males than in females; sides of neck and tail without red stripe in males ..... *P. montium*

Pholidobolus affinis (Peters)

New combination

Ecpleopus (*Aspidolaemus*) *affinis* Peters, 1862, Abh. Akad. Wiss. Berlin, 1862:199, pl. 3, fig. 1 [Holotype.—ZSM 664/0 from Pichincha Prov., Ecuador].[1]

[1] Through the courtesy of Thomas Uzzell, I recently examined the type specimen (ZMB 16593) of *Prionodactylus ocellifer* Werner, 1901. Uzzell and I agree that *Prionodactylus ocellifer* is a junior synonym of *Ecpleopus* (*Aspidolaemus*) *affinis* Peters, 1862.

Ecpleopus affinis—Boulenger, 1885, Cat. Liz. Brit. Mus., 2:402.

Aspidolaemus affinis—Uzzell, 1969, Postilla, 135:21.

Diagnosis.—1) Head width not sexually dimorphic; 2) head width/snout-vent length ratio 0.151-0.180 (0.162); 3) three supraoculars, the middle one being wedged between first and third with apex usually reaching superciliary row; 4) usually two prefrontals; 5) femoral pores present in about two percent of males; 6) lower eyelid scales opaque, three to six in number; 7) dorsals keeled to striated, seldom smooth; 8) lateral granules usually present at midbody; 9) lateral body fold present; 10) dorsolateral pale stripe extending to tip of snout; 11) body having black reticulations laterally on reddish orange ground color, lateral ocelli usually present; 12) sides of neck and tail without red stripe; 13) venter yellow in males; 14) venter pale yellow to gray in females; 15) underside of tail orange to orange-red in males.

Description and Color Pattern (140 individuals).—Maximum snout-vent length 64 mm for males, 58 mm for females. For details of scutellation and proportions see table 3 and generic definition.

Dorsum gray-brown to olive-brown with or without a dark brown to black middorsal stripe, or traces of it; dorsolateral stripe distinct, white to cream or yellow fading to pale gray posteriorly, edged with black, extending from snout along edge of orbit, terminating about midbody, in some individuals extending to near base of tail; labial stripe pale yellow or cream extending along upper lip to shoulder; side of head between dorsolateral and labial stripes uniform pale gray to dark brown; gular region dull white to yellowish; limbs gray-brown with fine black reticulation.

Males: Venter yellow to orange-red with scattered dark flecks posteriorly in some individuals; underside of tail orange to orange-red with or without brown or black flecks; flanks pale orange to orange-red with black reticulation resulting in indistinct ocelli; ventrolateral orange-red wash intensified in breeding males, extending high on flanks and dorsal surface of tail; iris tan to pale gold (Pl. 1A).

Females: Venter and underside of tail uniform pale yellow to pale or dark gray; usually orange-red color lacking; flanks pale brown, reticulated with black, or uniform dark brown or black; dorsal surface of tail brown to pale yellow.

Color differences among some populations are evident. Individuals from near Tixán have an orange-red, instead of yellow, venter; yellow is present on the chest of some individuals. Lizards from near Baños are noticeably pale; the venter is very pale yellow, and males have only faint traces of orange on the flanks. The nature of the middorsal stripe varies in local populations. For example, in 38 individuals from Mulaló, the stripe is distinct in 34, faint in three, and absent in one; in 16 individuals from southeast of Patate, the stripe is distinct in five, faint in nine, and absent in two individuals.

One specimen from Saraguro differs from all others examined. The belly and subcaudal areas are gray; the dorsum is tan, and the side of the head and neck are dark brown.

Distribution.—*Pholidobolus affinis* occurs principally in the Latacunga and Riobamba basins of the Central Valley. Mulaló is the northernmost record for the species. A single specimen taken at Saraguro probably represents a disjunct, relictual population. *Pholidobolus affinis* reaches the Pacific slopes of the Western Cordillera, penetrating at least as far as 3.3 km south of Tixán.

Pholidobolus prefrontalis new species

Holotype.—KU 141093 from 4.9 km, by road, south of Tixán, Chimborazo Province, Ecuador; obtained by R. R. Montanucci on 3 June 1971.

Paratypes.—KU 141094-141113, CAS 132583-84, USNM 193219-220 from 3.3-4.9 km south of Tixán, Chimborazo Province, Ecuador.

Diagnosis.—1) Head width not sexually dimorphic; 2) head width/snout-vent length ratio 0.150-0.177 (0.164); 3) two supraoculars, subequal in size; 4) usually two prefrontals; 5) femoral pores absent in both sexes; 6) lower eyelid scales opaque, three to six in number; 7) dorsals usually keeled; 8) lateral granules usually present at midbody; 9) lateral body fold present; 10) dorsolateral pale stripe extending to tip of snout; 11) sides of body with single, broad brown stripe, bordered by a pale stripe above and below, or several alternating brown and cream longitudinal stripes; 12) sides of neck and tail without red stripe; 13) venter gray to blue-black posteriorly in males; 14) venter gray or salmon in females; 15) underside of tail blue-black in males.

Description of Holotype.—Male, snout-vent length 50 mm; tail length 75 mm, partly regenerated; two prefrontals; four scales between the orbits; two supraoculars; 12 scales along upper lip; 12 scales along lower lip; 17 scales from mental to collar fold; 28 ventrals; 39 dorsals; six temporals; 39 scales around body; 19 scales around tail; 23 scales along forelimb; eight scales on third finger; six scales on fifth finger; 10 scales on third toe; 13 scales on fourth toe; nine scales on fifth toe; femoral pores absent; lateral granules present; lower eyelid opaque; four lower eyelid scales.

Dorsum uniform pale gray-brown; dorsolateral stripe pale yellow, extending from tip of snout to above forelimb; labial stripe white, extending to shoulder; sides of head and neck dark brown; flanks with single broad, brown stripe; narrow pale line extending from insertion of forelimb to hind limb; sides of tail with broad, brown stripe; light brown stripe extending dorsally on tail; chin, throat and chest salmon, blending into blue-black on belly and under tail (Pl. 1C).

Description and Color Pattern (109 individuals).—Maximum snout-vent length 57 mm for males, 63 mm for females. For details of scutellation and proportions see table 3 and generic definition.

Dorsum pale gray to dark brown (coppery cast evident in most young and sub-adults), with or without a dark brown to black middorsal stripe, or traces of it; middorsal brown zone with or without yellowish flecks; dorsolateral stripe white to yellow, edged with black dorsally, terminating above shoulder or grading imperceptibly into ground color near midbody; labial stripe yellow to white, terminating at forearm; pale cream lateral stripe extending beyond forearm to hind limb; single broad brown to dark brown stripe between dorsolateral and lateral cream stripes, or several brown stripes alternating with cream stripes; belly pink to salmon, or gray to blue-black with or without dark spots or flecks laterally and posteriorly; chin white to gray; underside of tail gray to blue-black.

Considerable variation exists in belly coloration between local populations and can be associated with geographic area. Among the populations on the Pacific slope, the belly color varies from gray-white (Guaranda) to light gray with pinkish cast (San José del Chimbo, two specimens) to a rich salmon (Alausí and Tixán). Males from the Alausí and Tixán populations have considerable blue-black or gray on the posterior belly, with salmon being restricted to the chest and throat. The belly color of the population at Cañar is pale gray. Varying amounts of ventral spotting are present among the samples from the Pacific slopes. At Guaranda, 26 individuals lack spots; seven have spots posteriorly. Most individuals in populations from the Cuenca Basin lack spotting, the venter being yellowish to dull white.

Polymorphism occurs in the nature of the middorsal stripe and number of lateral brown stripes (Table 6). In general, the samples from the Cuenca Valley have more brown stripes than those from the Pacific slopes. The amount of striping in a local sample apparently is associated with moisture. Prominently striped individuals are usually found at

mesic localities characterized by dense vegetation. More uniformly colored lizards occur in xeric, exposed areas. The color pattern probably has a cryptic function responding directly to predation. The pattern may also be involved with thermoregulation.

Distribution.—Pholidobolus prefrontalis occurs along the Pacific slopes of the Western Cordillera from Guaranda south to Cañar; populations are also found throughout the Cuenca Valley.

Etymology.—The specific name refers to the prominent prefrontal scales present in this species.

Pholidobolus montium (Peters)

Ecpleopus (*Pholidobolus*) *montium* Peters, 1862, Abh. Akad. Wiss. Berlin, 1862: 196, pl. 2, fig. 3.

Pholidobolus montium—Boulenger, 1885, Cat. Liz. Brit. Mus., 2:403.

Types.—The two syntypes used in the description of *Pholidobolus montium* represent two species. RMNH 3401 is hereby designated as the lectotype, because this specimen is from a known locality (Quito) and because Peters (1862) illustrated this specimen and used it for most of the type description. The other syntype (ZMB 900) from "western Ecuador" belongs to the species described in the next account.

Diagnosis.—1) Head width not sexually dimorphic; 2) head width/snout-vent length ratio 0.155-0.175 (0.163); 3) two supraoculars, subequal in size; 4) prefrontals absent; 5) femoral pores absent in both sexes; 6) lower eyelid scales opaque, three to six in number; 7) dorsals striated to smooth; 8) lateral granules present or absent at midbody; 9) lateral body fold present; 10) dorsolateral pale stripe extending to tip of snout; 11) several brown and cream longitudinal stripes on sides of body; 12) sides of neck and tail without red stripe; 13) venter light gray in males; 14) venter pale yellowish white to pale gray in females; 15) underside of tail gray to blue-black in males.

Description and Color Pattern (138 individuals).—Maximum snout-vent length 56 mm for males, 66 mm for females. For details of scutellation and proportions see table 3 and generic definition.

Dorsum pale gray to dark brown, with an iridescent coppery cast in many individuals; vertebral area with or without brown to black middorsal stripe, or brown to black flecks; dorsolateral stripe pale yellow, edged with dark brown or black, extending to above shoulder, or fading into dorsal dark field near midbody; labial stripe cream to white, extending to forearm; sides of head between labial and dorsolateral stripes uniform dark brown to black; sides of body with one or several brown to black-brown stripes alternating with several

TABLE 6. Polymorphism in lateral and middorsal stripes in samples of *Pholidobolus prefrontalis*. Frequency of each morph is expressed as a percentage of the sample size at each locality. Sample size is indicated in parentheses.

Sample	Number of dark lateral stripes				Nature of middorsal stripe		
	1	2	3	4	Absent	Trace	Present
Guaranda (33)	21.2	57.6	21.2	----	57.6	36.3	6.1
Alausí (16)	100	----	----	----	50.0	50.0	----
Tixán (24)	100	----	----	----	70.9	20.8	8.3
Cutchil (13)	----	7.8	61.5	30.7	7.7	23.1	69.2

PLATE 1. A. *Pholidobolus affinis* ♂ (KU 140983; 55 mm SVL) from 8.9 km SSE Patate; B. *P. montium* ♂ (KU 141081; 55 mm SVL) from 2.5 km E Río Chiche; C. *P. prefrontalis* ♂ (KU 141093, holotype; 50 mm SVL) from 4.9 km S Tixán; D. *P. macbrydei* ♂ (KU 140993, holotype; 53 mm SVL) from 9.1 km N, 2.3 km W Biblián; E. *P. annectens* ♀ (KU 140986; 55 mm SVL) from Loja Valley. Photos by George R. Pisani.

PLATE 1

A

B

C

D

E

TABLE 7. Polymorphism in lateral stripes in samples of *Pholidobolus montium*. Frequency of each morph is expressed as a percentage of the sample size at each locality. Sample size is indicated in parentheses.

Sample	Number of dark lateral stripes					
	1	2	3	4	5	6
Ibarra (20)	10.0	35.0	50.0	5.0	-----	-----
Otavalo (33)	-----	-----	63.6	36.4	-----	-----
Cayambe (38)	28.9	28.9	34.2	8.0	-----	-----
W San Antonio (20)	5.0	5.0	60.0	30.0	-----	-----
San Antonio (17)	-----	17.6	64.8	17.6	-----	-----
Quito (14)	-----	28.5	71.5	-----	-----	-----
Lago Cuicocha (20)	-----	-----	5.0	10.0	80.0	5.0
E Río Chiche (31)	6.4	9.7	12.9	61.3	9.7	-----

white, cream or yellowish stripes (Pl. 1B); chin and throat dull white to pale gray; venter pale yellowish white to iridescent pale gray, with or without black spots or flecks posteriorly and laterally; underside of tail gray to blue-black.

The number of lateral brown stripes is variable; frequencies of various numbers in different local populations are shown in table 7. The number of lateral stripes may be associated with moisture and vegetative characteristics of the locality, presumably in response to predator pressure. However, the relationship between amount of striping and vegetation is not as obvious as in *Pholidobolus prefrontalis*. Polymorphism in the nature of the middorsal stripe and ventral pattern is summarized in table 8. There is no evidence to indicate that ventral spotting varies ontogenetically. The insular population from Lago Cuicocha shows slight differences in ventral coloration compared to surrounding samples. The chest color is pale orangish yellow in five of eight males examined. Among 12 females, only three have the yellowish color, whereas nine have the typical grayish color with or without an iridescent cast.

Distribution.—Pholidobolus montium occurs in the northern basins of Quito, Ibarra, and adjacent valleys, and is expected in extreme southern Colombia. The southern limit of its distribution is near the northern end of the Central Valley (Latacunga Basin) near Mulaló. A more southern record from near Baños needs confirmation; I searched the Baños area unsuccessfully for additional specimens.

Pholidobolus macbrydei new species

Holotype.—KU 140993 from 9.1 km north and 2.3 km west (by road) of Biblián, near Hacienda Oeste, 3070 m,

TABLE 8. Polymorphism in middorsal stripe and ventral pattern in samples of *Pholidobolus montium*. Frequency of each morph is expressed as a percentage of the sample size at each locality. Sample size is indicated in parentheses.

Sample	Nature of middorsal stripe			Ventral pattern			
	Absent	Trace	Present	Uniform light gray	Posterior half spotted	Totally spotted	Uniform black
Ibarra (20)	20.0	60.0	20.0	60.0	25.0	15.0	-----
Otavalo (33)	-----	54.5	45.5	36.4	48.5	9.0	6.1
Cayambe (38)	39.5	31.6	28.9	76.3	23.7	-----	-----
W San Antonio (20)	10.0	55.0	35.0	45.0	50.0	5.0	-----
San Antonio (17)	29.4	58.8	11.8	94.1	5.9	-----	-----
Quito (14)	14.2	35.7	50.1	21.4	42.9	35.7	-----
Lago Cuicocha (20)	5.0	30.0	65.0	75.0	25.0	-----	-----
E Río Chiche (31)	9.7	87.1	3.2	19.3	71.0	9.7	-----

Cañar Province, Ecuador; obtained by R. R. Montanucci and B. MacBryde on 23 May, 1971.

Paratypes.—KU 140994-141014, CAS 132581, USNM 193217 from 14.2 km north (by road) of Biblián, 3430 m, and KU 141015-141027, CAS 132582, USNM 193218 from 9.1 km north and 2.3 km west (by road) of Biblián, near Hacienda Oeste, 3070 m, Cañar Province, Ecuador.

Diagnosis.—1) Head width distinctly greater in males than in females; 2) head width/snout-vent length ratio 0.164-0.204 (0.183) which is significantly greater than that of *P. montium* ($t = 6.72$; $P < .001$); 3) two supraoculars, subequal in size; 4) prefrontals absent or present; 5) femoral pores usually present in males; 6) lower eyelid scales opaque, three to six in number; 7) dorsals usually smooth to striated; 8) lateral granules present or absent at midbody; 9) lateral body fold present; 10) dorsolateral pale stripe not extending to tip of snout; 11) sides of body with several brown stripes alternating with cream stripes; 12) sides of neck and tail with bright red stripe in males; 13) venter pale gray to charcoal in males; 14) venter bright yellow or orange-red in females; 15) underside of tail blue-black in males.

Description of Holotype.—Male, snout-vent length 53 mm, tail length 74 mm, partly regenerated; prefrontals absent; four scales between the orbits; two supraoculars; 11 scales along upper lip; ten scales along lower lip; 15 scales from mental to collar fold; 24 ventrals; 39 dorsals; five temporals; 32 scales around body; 21 scales around tail; 20 scales along forelimb; eight scales on third finger; five scales on fifth finger; eight scales on third toe; 11 scales on fourth toe; eight scales on fifth toe; five femoral pores total; lateral granules present; lower eyelid opaque; five lower eyelid scales.

Dorsum pale yellowish brown with a black vertebral stripe; a paravertebral stripe on either side extending from occiput to rump; dorsolateral, pale yellowish tan stripe extending from outer margin of orbit to base of tail; labial stripe white, edged with black, extending posteriorly to insertion of forelimb; two broad, gray-brown stripes on either side of body, separated by a pale yellowish brown stripe; red stripe extending from ear opening to above insertion of forelimb; broad red stripe on sides of tail, extending from near insertion of hind limb posteriorly, fading distally on tail; belly and underside of tail charcoal; chin and throat iridescent dull white with gray flecks posteriorly (Pl. 1D).

Description and Color Pattern (114 individuals).—Maximum snout-vent length 56 mm for both sexes. For details of scutellation and proportions see table 3 and generic definition.

Dorsum gray-brown, yellowish brown to dark brown; vertebral area with or without brown to black middorsal stripe, or black spots; sides of body uniform brown, or with several brown to black longitudinal stripes alternating with dull white to cream stripes; dorsolateral stripe cream to yellow, extending posteriorly to above shoulder or midbody; anteriorly, dorsolateral stripe terminating near posterior or anterior corner of ocular orbit; labial stripe cream or white, extending to forearm; chin and throat pale iridescent gray to pale yellowish bronze; underside of tail blue-black.

Males: Bright red stripe extending from above forearm anteriorly to ear opening; sides of tail with broad red stripe; venter pale gray with or without dark gray to black flecks or spots posteriorly; ventral spotting extensive in some specimens, producing nearly uniform charcoal belly.

Females: Sides of neck and tail brown or orange-brown; exceptionally highly colored females with red in these areas; belly color polymorphic: bright yellow or orange-red with or without black spots posteriorly; relative frequencies of yellow and red belly morphs three to one respectively.

Populations of *Pholidobolus mac-*

brydei from near Saraguro south to east of Loja are distinctive. The brown tones of the dorsum are dark and have a coppery, iridescent cast. The dorsolateral and labial stripes are also iridescent, having a distinct greenish to bluish cast. The red stripe on the sides of the neck in males is more extensive in the southern than northern populations, usually extending anteriorly to the posterior edge of the eye in southern individuals. The belly in males is pale reddish pink to red with varying amounts of black mottling. In females, the belly color is iridescent dull yellow; the orange-red belly morph seemingly is absent in the southern populations. In juveniles, the belly varies from grayish to yellowish bronze.

The picture of color variation in the southern populations is complicated by the presence of a morph lacking red stripes on the neck and tail. The vertebral area of this morph is pale uniform gray; the flanks are brown. In males, the sides of the neck are reddish brown in some specimens. The belly in males is pinkish bronze; the underside of the tail is reddish orange with black spots. In females the belly is grayish bronze. This atypical morph has been collected 6 km north of San Lucas and on the crest of the Eastern Cordillera between Zamora and Loja. At both localities, it occurs with individuals of the usual color pattern; the numbers of the atypical morph are relatively restricted in comparison to the numbers of more typically colored individuals. In northern populations, the red stripes on the neck and tail are present but noticeably dull in males from 8-12 km south of Cutchil.

Polymorphism in the nature of the middorsal stripe among selected samples can be summarized as follows: the stripe is absent in all of 16 specimens from 13-15 km east of Loja; in a sample of 16 lizards from 8-12 km south of Cutchil, the middorsal stripe is absent in seven and faint in nine individuals; in 19 individuals from 14.2 km north of Biblián, the stripe is distinct in 15, faint in three, and absent in one; among 15 specimens from 9.1 km north of Biblián, the stripe is distinct in six, faint in two and absent in seven individuals. The differences in striping among these samples cannot be associated with any differences in vegetation among the localities.

Distribution.—*Pholidobolus macbrydei* is known from the crests and slopes of the Western and Eastern Cordilleras and the connecting spurs and ridges. The northernmost record is Urbina, Chimborazo Province. The southernmost locality is the crest of the Eastern Cordillera between Zamora and Loja.

Etymology.—This species is named for Dr. Bruce MacBryde, formerly of Universidad Católica del Ecuador, Quito, who provided invaluable field assistance.

Remarks.—*Pholidobolus macbrydei* from the mountain crest between Zamora and Loja can be confused with *P. prefrontalis* because of the high frequency of prefrontals and the tendency for the red color on the neck and tail to fade rapidly in preservative. One must rely on the presence of femoral pores in males or the absence of the dorsolateral stripe on the tip of the snout in both sexes to distinguish southern examples of *macbrydei* from *prefrontalis*.

Pholidobolus annectens (Parker)

New combination

Macropholidus annectens Parker, 1930, Ann. Mag. Nat. Hist., (10) 5:569. Holotype.—BMNH 1930.1.30.2 from vicinity of Loja, Ecuador, 2200 m.

Diagnosis.—1) Head width not sexually dimorphic; 2) head width/snout-vent length ratio 0.154-0.166 (0.161); 3) two supraoculars, subequal in size; 4) prefrontals absent; 5) femoral pores present in about 26 percent of males; 6) lower eyelid usually a single disc, transparent or with varying amounts of pigmentation; 7) dorsal scales striated to weakly keeled; 8) lateral granules usually absent at midbody; 9) lateral body fold absent; 10) dorsolateral pale stripe extending to tip of snout, but faint and narrow; 11) sides of body uniformly gray

to gray-brown; 12) sides of neck and tail with flecks of orange-red in some males; 13) venter pale orange-bronze in males; 14) venter white or pale yellow in females; 15) underside of tail pale pink to orange in males.

Description and Color Pattern (21 individuals).—Maximum snout-vent length 53 mm for males, 60 mm for females. For details of scutellation and proportions see table 3 and generic definition.

Dorsum uniform pale brown, gray-brown, or pale blue-gray; dorsolateral stripe narrow, pale yellow to cream or white, edged with dark gray or black, extending from snout to above shoulders or midbody (Pl. 1E); faint traces of labial stripe in some specimens; underside of tail flecked with charcoal gray or black.

Males: Traces or flecks of orange-red on sides of neck and tail; venter pale orange-bronze; underside of tail pale pink to orange.

Females: Traces of orange-red absent laterally; belly and throat yellow to gray or white.

Juveniles: Ocelli on sides of neck; dark flecks on limbs.

Distribution.—Known only from Loja Valley in southern Ecuador.

SUMMARY

The genus *Pholidobolus* is a montane group of microteiid lizards known only from the Andean region of Ecuador. I recognize five species on the basis of concordant variation among independent character states and sympatry in several localities between phenetically distinct and otherwise allopatric populations.

Sums of Squares Simultaneous Test Procedure (Power, 1970) was used to describe major trends of variation within the species. In *Pholidobolus affinis* high mean values for most meristic characters are present in geographically central samples, whereas, lower counts are characteristic of peripheral samples from the north, southwest, and east. In *Pholidobolus macbrydei,* four characters vary clinally, showing an increase in mean values from north to south with or without slight reversals. In two characters, a sharp step in the cline occurs south of Saraguro. Samples of *Pholidobolus prefrontalis* show no general geographical trends. *Pholidobolus montium* exhibits relatively low mean values for most meristic characters in extreme northern and southern samples.

Correlation analysis was applied to 20 morphological characters and three ecological parameters (rainfall, temperature and elevation), as well as geographical distance; it revealed an inverse correlation between precipitation and four meristic characters and a weak positive correlation with one meristic character. A significant positive correlation also exists between patristic distance (weighted character divergence) among local samples and the rainfall dissimilarity of their localities.

All species of *Pholidobolus* are oviparous, and usually deposit two eggs per clutch. Courtship and mating patterns are nearly identical among the five species. Members of the genus are diurnal, basking, and foraging lizards. Their ecological roles are essentially equivalent; however, there are apparent differences in moisture tolerances. *Pholidobolus macbrydei* is the most mesic-adapted species, occurring in montane forest and wet páramo habitats. *Pholidobolus montium* also occurs in mesic habitats but shows tolerance for drier situations. Likewise, *Pholidobolus annectens* inhabits relatively drier situations in the Loja Basin. *Pholidobolus prefrontalis* is ecologically specialized, occurring in the relatively arid Pacific slopes and Cuenca Basin. *Pholidobolus affinis* is considered to be ecologically generalized; it exhibits a broad moisture tolerance.

The distributions of all species of *Pholidobolus* are characteristically allopatric or parapatric. Where zones of

contact exist, they are narrow. Presumably, sympatry over extensive areas is not possible because of equivalent ecological roles played by the species. Due to environmental differences between geographic areas and the adaptive superiority of each species in its respective area, encroachment and displacement among the species is apparently prevented. Discriminant Function Analysis applied to sympatric samples suggests that hybridization seldom occurs if at all.

Quantitative Phyletic Analysis (Kluge and Farris, 1969) was employed to infer the evolutionary relationships among the species of *Pholidobolus*. Based on the criteria of Wagner (1961), *Pholidobolus affinis* is considered most primitive in its suite of character states. The other species are progressively derived, with *P. annectens* being the most derived-specialized member of the genus. Ecological information tends to support this arrangement. A Wagner Diagram generated from 29 OTUs (local samples) of *Pholidobolus* reveals that an *affinis*-like ancestor gave rise to a generalized-derived *montium*-like stock which in turn underwent evolutionary radiation, producing several ecologically or morphologically specialized species. The major diversification of *Pholidobolus* is believed to have occurred during the Pleistocene. Geographical and ecological barriers have been implicated in most Andean patterns of speciation (Vuilleumier, 1971). However, in *Pholidobolus*, divergence through isolation is not the simplest interpretation. On the contrary, natural selection rather than isolation is considered to be the primary evolutionary force. Several lines of evidence support this argument: 1) There is no correlation between geographical proximity and morphological similarity among intraspecific samples. 2) Maximal glacial extent depicted by Sauer (1965) would not have formed complete barriers to dispersal between basins. 3) Vegetative barriers are unlikely since the species of *Pholidobolus* have overlapping moisture tolerance limits and most inhabit several vegetative associations. Therefore, patterns of divergence in the genus are attributed to differential selective regimes acting upon the populations.

The following taxonomic changes have been made: *Aspidolaemus* Peters 1862 = *Pholidobolus* Peters 1862; *Aspidolaemus affinis* Peters 1862 = *Pholidobolus affinis* new combination; *Macropholidus annectens* Parker 1930 = *Pholidobolus annectens* new combination. Two new species are named: *Pholidobolus prefrontalis* and *Pholidobolus macbrydei*.

RESUMEN

El género *Pholidobolus* es un grupo de lagartos microteiidos que se hallan únicamente en la región andina del Ecuador. Yo reconozco solamente cinco especies basado en la armonía geográfica de las características con diferentes grados y la simpatría en varias localidades de las poblaciones feneticamente distintas.

El método usado para describir las principales tendencias de variación dentro de cada especie es el llamado SS-STP (Power, 1970). En *Pholidobolus affinis* las muestras de las localidades centrales presentan un alto valor en los promedios para la mayoría de las características discontínuas; por el contrario en las muestras de la periferia hacia el norte, sureste y este tienen un valor bajo. En *Pholidobolus macbrydei*, cuatro características demuestran una variación clinal, aumentando el valor de los promedios de norte a sur, a veces con pequeñas variaciones inversas. En dos características la variación clinal sufre un cambio drástico al sur de Saraguro. En las muestras de *Pholidobolus prefrontalis* no hay ninguna indicación de tendencias geográficas. En *Pholidobolus montium* los valores de los promedios son relativamente bajos para la mayoría de las car-

acterísticas discontinuas en las muestras del extremo norte y sur de la región.

El análisis de correlación aplicado a 20 características morfológicas y tres parámetros ecológicos (lluvia, temperatura y altura) como también distancia geográfica, indica una correlación inversa entre precipitación y cuatro características y una correlación relativamente debil con una característica. Una correlación significativamente positiva existe también entre la distancia "patristica" (caracter cargado de divergencia Kluge y Farris, 1969) entre las muestras locales y la diferencia en lluvia en las respectivas localidades.

Todas las especies de *Pholidobolus* son ovíparas, y usualmente depositan dos huevos en cada nidada. Los patrones del cortejo y apareamiento son idénticos o casi idénticos entre las cinco especies. Los miembros del género son lagartos diurnos, que termoregulan exponiendose al sol, y se alimentan buscando el alimento. Sus papeles ecológicos son esencialmente equivalentes; sin embargo, hay aparente divergencias en la tolerancia a la humedad. *Pholidobolus macbrydei* es la especie mas adaptada a un habitat húmedo. *Pholidobolus montium* también se encuentra en habitats húmedos, pero muestra una tolerancia a situaciones más secas. Del mismo modo *Pholidobolus annectens* habita usualmente regiones relativamente más secas en el valle de Loja. *Pholidobolus prefrontalis* es especializado ecologicamente, encontrándose en las regiones áridas en las cuestas del Pacífico y en el valle de Cuenca. *Pholidobolus affinis* se considera que es ecologicamente generalizado, y exhibe una tolerancia muy amplia para la humedad.

La distribución de todas las especies de *Pholidobolus* es caracteristicamente allopátrica o parapátrica; pero en las areas donde existe zonas de contacto son angostas. Posiblemente, la simpatría no es posible en areas muy extensas debido a los papeles ecológicos equivalentes que cada especie desempeña. Debido a las diferencias medio ambientales entre las areas geográficas y la gran adaptabilidad de cada especie en su respectiva región aparentemente se previene el desplazamiento entre las especies. Al aplicar el análisis de funciones discriminantes a muestras simpátricas se sugiere que en estes poblaciones nunca ocurre la hibridisación.

El análisis filético cuantitativo (Kluge y Farris, 1969) fué empleado para deducir las relaciones evolutivas dentro las especies de *Pholidobolus*. Basado en el criterio de Wagner (1961), *Pholidobolus affinis* se considera como la especie más primitiva por sus características. Las otras especies se derivan progresivamente, siendo *P. annectens* la derivación más avanzada dentro de los miembros del género. La información ecológica tiende a sustentar este arreglo. Usando el diagrama de Wagner generado por 29 OTUs (muestras locales) de *Pholidobolus*, demuestra que un ancestro parecido a *affinis* dío lugar a un tipo más generalizado, el grupo parecido a *montium*, que a su vez sufrió una radiación evolutiva produciendo varias especies ecológicamente y morfológicamente especializadas. La mayor diversificación de *Pholidobolus* se cree que ocurrió durante el Pleistoceno. Las barreras geográficas y ecológicas han influído en la mayoría de los patrones de especiación en los Andes (Vuilleumier, 1971). Sin embargo en *Pholidobolus* la divergencia a través de aislamiento no es necesariamente la interpretación mas sencilla. Por el contrario, en lugar de aislamiento es la selección natural la que ha influído como fuerza primaria en la evolución. Varias lineas de evidencia sustentan este argumento: 1) no hay correlación entre proximidad geográfica y la similitud morfológica entre muestras intraespecíficas; 2) la máxima extensión glacial sugerida por Sauer (1965) no ha formado barreras completas a la dispersión de animales entre los valles; 3) las barreras vegetativas son improvables, puesto que las especies de *Pholidobolus* tienen límites de tolerancia a la humedad que se extienden el uno sobre el otro y la mayoría habitan varias asociaciones vegetativas.

Por lo tanto, los patrones de divergencia en el género son atribuidos a regímenes diferenciales selectivos que actuan sobre las poblaciones.

Los siguientes son los cambios taxonómicos que se han hecho: *Aspidolaemus* Peters 1862 = *Pholidobolus* Peters 1862; *Aspidolaemus affinis* Peters 1862 = *Pholidobolus affinis* nueva combinación; *Macropholidus annectens* Parker 1930 = *Pholidobolus annectens* nueva combinación. Se nombran dos nuevas especies: *Pholidobolus prefrontalis* y *Pholidobolus macbrydei*.

APPENDIX A

SUMMARY OF STATISTICS

Tables 9-23 summarize the basic statistics for local samples of *Pholidobolus* studied herein and provide the results of Simultaneous Test Procedure (STP) analysis. Statistically homogeneous subsets determined through STP analysis are delimited by vertical lines in the tables. Local samples are designated according to species as follows: *P. affinis* (a), *P. annectens* (n), *P. macbrydei* (c), *P. montium* (m), and *P. prefrontalis* (p). Local samples are also designated alphabetically (in capital letters) from north to south within the geographic range of each species. Thus Ac would be the northernmost sample of *P. macbrydei.*

TABLE 9. Number of Lower Eyelid Scales (LES).

SAMPLE	N	RANGE	$\bar{X}$	SD	$2SE_{\bar{X}}$	STP
Ca	19	3-5	4.1	0.66	0.302	
Fa	30	3-6	4.0	0.76	0.279	
Ga	18	3-5	3.8	0.71	0.333	
Ba	6	3-4	3.8	0.41	0.333	
Da	11	3-4	3.7	0.47	0.282	
Ia	14	3-5	3.7	0.61	0.327	
Ea	16	3-4	3.6	0.50	0.250	
Aa	38	3-4	3.5	0.51	0.164	
Ha	6	3-4	3.3	0.52	0.422	
Cp	16	3-5	4.4	0.62	0.310	
Bp	29	3-6	4.2	0.58	0.214	
Dp	9	3-5	4.1	0.60	0.401	
Fp	11	3-5	4.1	0.54	0.325	
Ep	12	3-5	3.6	0.65	0.376	
Ap	31	3-5	3.6	0.61	0.218	
Bm	54	3-5	4.4	0.62	0.169	
Cm	52	3-5	4.2	0.54	0.149	
Hm	8	3-5	4.1	0.64	0.453	
Em	17	3-6	4.1	0.78	0.379	
Dm	20	3-5	4.1	0.55	0.247	
Gm	31	3-5	4.1	0.47	0.170	
Am	23	3-5	4.1	0.73	0.306	
Fm	21	3-5	3.8	0.60	0.263	
Ec	20	3-6	4.4	0.68	0.304	
Bc	23	3-6	4.3	0.81	0.169	
Cc	21	3-5	4.2	0.68	0.297	
Dc	20	3-5	4.1	0.51	0.228	
Ac	7	3-4	3.6	0.53	0.404	
An	26	1-2	1.0	0.20	0.077	

TABLE 10. Number of Scales Along Upper Jaw (SUJ).

SAMPLE	N	RANGE	$\bar{X}$	SD	$2SE_{\bar{x}}$	STP
Da	11	13-14	13.6	0.51	0.304	
Ca	19	13-14	13.4	0.51	0.233	
Fa	30	12-15	13.2	0.68	0.247	
Ba	6	12-14	13.0	0.63	0.516	
Ea	16	11-14	12.8	0.68	0.342	
Ha	6	12-13	12.6	0.52	0.421	
Ia	14	12-14	12.6	0.65	0.345	
Ga	18	12-14	12.6	0.62	0.290	
Aa	38	11-14	12.4	0.59	0.191	
Dp	9	11-13	12.1	0.78	0.521	
Bp	29	11-14	11.9	0.59	0.220	
Cp	16	11-12	11.5	0.51	0.256	
Ap	31	10-12	11.3	0.53	0.190	
Ep	12	10-12	10.8	0.75	0.435	
Fp	11	9-11	9.9	0.54	0.325	
Em	17	11-14	12.4	0.70	0.340	
Dm	20	11-14	12.0	0.83	0.369	
Gm	31	11-13	11.9	0.50	0.179	
Fm	21	11-13	11.6	0.60	0.261	
Cm	52	10-13	11.4	0.56	0.156	
Am	23	10-13	11.3	0.74	0.313	
Hm	8	10-12	11.0	0.54	0.378	
Bm	54	10-13	11.0	0.81	0.221	
Ec	20	10-13	12.1	0.89	0.397	
Dc	20	10-12	11.3	0.55	0.246	
Cc	21	9-12	10.8	0.68	0.297	
Ac	7	10-11	10.7	0.49	0.369	
Bc	23	9-13	10.7	0.11	0.446	
An	26	11-12	11.6	0.50	0.195	

TABLE 11. Number of Scales Along Lower Jaw (SLJ).

SAMPLE	N	RANGE	$\bar{X}$	SD	$2SE_{\bar{x}}$	STP
Ca	19	13-14	13.5	0.51	0.235	
Da	11	12-14	13.3	0.65	0.390	
Ba	6	12-14	13.2	0.75	0.615	
Fa	30	11-14	12.7	0.66	0.241	
Ha	6	11-13	12.3	0.82	0.667	
Ea	16	11-14	12.3	0.87	0.437	
Aa	38	11-14	12.3	0.65	0.212	
Ia	14	11-14	12.2	0.80	0.429	
Ga	18	11-13	12.2	0.79	0.370	
Dp	9	11-13	11.8	0.83	0.556	
Bp	29	11-12	11.6	0.50	0.186	
Cp	16	10-13	11.1	0.72	0.359	
Fp	11	10-12	11.1	0.54	0.325	
Ap	31	10-13	11.0	0.68	0.245	
Ep	12	10-12	11.0	0.85	0.492	
Em	17	10-14	12.2	1.01	0.492	
Dm	20	11-12	11.8	0.41	0.184	
Gm	31	10-13	11.5	0.62	0.224	
Fm	21	10-13	11.4	0.68	0.295	
Cm	52	10-13	11.2	0.78	0.217	
Hm	8	10-12	10.9	0.64	0.453	
Am	23	10-12	10.8	0.65	0.271	
Bm	54	9-12	10.4	0.79	0.216	
Ec	20	10-15	11.9	1.09	0.487	
Dc	20	10-12	11.2	0.67	0.300	
Ac	7	10-12	10.7	0.76	0.571	
Bc	23	9-12	10.7	0.83	0.347	
Cc	21	9-11	10.4	0.75	0.326	
An	26	10-13	10.8	0.76	0.300	

TABLE 12. Number of Scales Between Collar Fold and Chin (SGJ).

SAMPLE	N	RANGE	$\bar{X}$	SD	$2SE_{\bar{X}}$	STP
Fa	30	20-26	22.5	1.50	0.549	
Da	11	21-25	22.5	1.36	0.825	
Ca	19	20-25	21.9	1.19	0.549	
Ia	14	19-23	21.9	1.23	0.658	
Ea	16	20-24	21.6	1.31	0.657	
Ha	6	19-22	21.2	1.16	0.955	
Ba	6	19-23	21.0	1.78	1.46	
Aa	38	18-24	20.4	1.22	0.397	
Ga	18	16-22	19.3	1.57	0.741	
Dp	9	17-20	18.8	0.97	0.648	
Fp	11	17-19	17.5	0.69	0.414	
Ep	12	15-19	17.3	1.07	0.620	
Bp	29	15-18	16.9	1.03	0.381	
Cp	16	15-18	16.6	0.72	0.359	
Ap	31	15-18	16.1	0.75	0.268	
Em	17	18-21	19.4	0.93	0.452	
Dm	20	17-20	18.7	0.86	0.387	
Gm	31	16-21	18.5	1.03	0.369	
Cm	52	16-22	18.0	1.20	0.334	
Fm	21	17-19	17.9	0.77	0.335	
Bm	54	15-19	17.4	1.06	0.288	
Am	23	16-19	17.4	0.89	0.371	
Hm	8	15-18	16.6	0.92	0.648	
Ec	20	16-22	18.8	1.91	0.853	
Dc	20	15-18	16.5	1.00	0.447	
Bc	23	15-18	16.4	0.72	0.301	
Cc	21	13-18	16.4	1.16	0.506	
Ac	7	15-16	15.6	0.53	0.404	
An	26	15-20	17.7	1.28	0.503	

TABLE 13. Number of Scales from Collar Fold to Vent (SGV).

SAMPLE	N	RANGE	$\bar{X}$	SD	$2SE_{\bar{X}}$	STP
Da	11	31-35	32.1	1.22	0.736	
Fa	30	30-33	31.3	1.16	0.423	
Ba	6	30-33	31.2	1.17	0.955	
Ea	16	29-34	30.8	1.33	0.644	
Ga	18	29-32	30.3	1.03	0.485	
Ca	19	29-32	30.2	0.98	0.448	
Ia	14	29-31	29.8	0.80	0.429	
Ha	6	28-31	29.7	1.03	0.843	
Aa	38	27-32	29.3	1.11	0.362	
Dp	9	28-32	30.1	1.17	0.778	
Fp	11	25-30	28.5	1.44	0.868	
Ep	12	27-29	28.4	0.67	0.386	
Bp	29	26-30	28.3	1.28	0.475	
Cp	16	26-29	27.4	1.03	0.515	
Ap	31	24-28	26.8	0.93	0.336	
Dm	20	27-31	28.4	0.99	0.442	
Em	17	26-30	28.3	1.05	0.508	
Fm	21	26-30	27.8	1.40	0.611	
Gm	31	25-30	27.7	1.18	0.425	
Am	23	26-29	27.6	1.03	0.431	
Cm	52	25-30	27.5	1.18	0.327	
Hm	8	26-28	27.1	0.83	0.590	
Bm	54	24-30	26.6	1.28	0.349	
Ac	7	25-28	25.9	1.21	0.918	
Oc	20	23-28	25.3	1.38	0.617	
Ec	20	23-28	25.3	1.48	0.663	
Cc	21	23-28	24.8	1.33	0.579	
Bc	23	23-28	24.8	1.31	0.547	
An	26	25-30	27.3	1.26	0.493	

TABLE 14. Number of Dorsal Scales (DEL).

SAMPLE	N	RANGE	$\bar{X}$	SD	$2SE_{\bar{X}}$	STP
Da	11	50-54	52.5	1.44	0.868	
Ha	6	50-54	51.7	1.63	1.333	
Ca	19	47-53	50.4	1.54	0.706	
Fa	30	47-54	50.4	2.19	0.800	
Ba	6	49-52	50.3	1.21	0.989	
Ia	14	46-52	49.8	1.85	0.987	
Aa	38	46-54	49.4	1.67	0.542	
Ea	16	45-55	49.3	2.60	1.300	
Ga	18	45-50	47.4	1.65	0.778	
Ep	12	41-49	45.3	2.42	1.395	
Fp	11	38-46	42.5	2.50	1.510	
Dp	9	38-46	41.6	2.35	1.567	
Bp	29	37-46	40.1	2.20	0.817	
Cp	16	37-43	39.6	1.75	0.875	
Ap	31	37-45	39.5	1.89	0.681	
Em	17	44-50	46.2	1.63	0.790	
Dm	20	43-50	46.1	2.10	0.939	
Cm	52	37-50	44.2	2.86	0.794	
Gm	31	41-47	44.0	1.68	0.605	
Am	23	39-47	43.6	1.99	0.832	
Fm	21	40-48	43.6	1.89	0.823	
Hm	8	40-44	42.0	1.41	1.000	
Bm	54	35-47	40.7	2.15	0.585	
Ec	20	35-43	39.6	1.96	0.876	
Ac	7	36-43	38.9	2.41	1.820	
Dc	20	35-41	37.9	1.55	0.694	
Cc	21	31-39	35.6	1.86	0.811	
Bc	23	33-37	35.5	1.34	0.560	
An	26	40-48	42.6	1.90	0.746	

TABLE 15. Number of Temporal Scales (NTS).

SAMPLE	N	RANGE	$\bar{X}$	SD	$2SE_{\bar{X}}$	STP
Fa	30	7-10	8.3	0.88	0.323	
Da	11	7-9	8.2	0.87	0.530	
Ia	14	7-9	8.0	0.78	0.419	
Ca	19	7-10	8.0	0.94	0.433	
Ea	16	6-10	7.8	0.91	0.455	
Aa	38	7-9	7.6	0.65	0.209	
Ba	6	7-9	7.5	0.84	0.683	
Ga	18	6-9	7.3	0.96	0.452	
Ha	6	5-8	6.3	1.21	0.989	
Cp	16	6-9	7.1	0.72	0.359	
Dp	9	5-8	6.4	1.01	0.676	
Bp	29	5-7	6.0	0.50	0.185	
Fp	11	5-6	5.5	0.52	0.315	
Ep	12	5-6	5.4	0.51	0.297	
Ap	31	5-7	5.3	0.58	0.207	
Em	17	6-8	6.6	0.62	0.300	
Dm	20	5-8	6.5	0.83	0.369	
Cm	52	4-8	6.3	0.68	0.188	
Am	23	5-7	6.2	0.52	0.216	
Fm	21	4-7	5.6	0.81	0.354	
Bm	54	5-7	5.5	0.61	0.165	
Gm	31	5-6	5.4	0.51	0.182	
Hm	8	5-6	5.3	0.46	0.327	
Ec	20	5-8	6.2	0.89	0.400	
Dc	20	4-7	5.6	0.75	0.337	
Bc	23	4-5	4.9	0.29	0.120	
Ac	7	4-5	4.9	0.38	0.286	
Cc	21	4-6	4.9	0.57	0.250	
An	26	5-8	6.5	0.65	0.254	

TABLE 16. Number of Scales Around Body (SAB).

SAMPLE	N	RANGE	$\bar{X}$	SD	$2SE_{\bar{X}}$	STP
Da	11	46-53	50.0	1.90	1.144	
Fa	30	45-54	49.7	2.25	0.820	
Ba	6	44-54	47.8	3.31	0.270	
Ca	19	41-51	44.9	2.41	1.108	
Ea	16	41-51	44.9	3.40	1.698	
Ia	14	39-43	40.9	1.38	0.740	
Aa	38	38-46	40.7	1.80	0.584	
Ha	6	36-40	38.7	1.37	1.115	
Ga	18	34-43	38.2	2.37	1.115	
Dp	9	38-42	40.4	1.42	0.949	
Bp	29	35-45	40.4	1.90	0.705	
Cp	16	36-42	38.6	2.03	1.014	
Ep	12	34-41	37.6	2.27	1.313	
Fp	11	34-40	36.8	2.04	1.230	
Ap	31	31-40	36.5	2.11	0.758	
Em	17	39-45	42.1	2.36	1.144	
Dm	20	37-44	40.2	1.84	0.824	
Cm	52	32-42	37.5	2.28	0.632	
Gm	31	33-41	37.4	1.87	0.673	
Hm	8	35-38	36.4	1.19	0.840	
Fm	21	32-39	35.5	2.04	0.890	
Am	23	32-38	35.1	1.86	0.774	
Bm	54	31.40	35.0	2.15	0.586	
Ec	20	33-41	37.0	2.10	0.940	
Dc	20	29-39	33.6	2.37	1.060	
Cc	21	28-35	31.6	1.43	0.625	
Bc	23	27-34	30.8	1.65	0.688	
Ac	7	27-32	30.3	2.06	1.556	
An	26	23-29	26.5	1.14	0.447	

TABLE 17. Number of Scales Around Tail (SAT).

SAMPLE	N	RANGE	$\bar{X}$	SD	$2SE_{\bar{X}}$	STP
Da	11	28-33	30.5	3.02	0.909	
Fa	30	26-33	29.8	1.56	0.568	
Ea	16	26-33	29.6	2.16	1.080	
Ca	19	27-31	29.4	1.12	0.512	
Ba	6	27-34	29.3	2.50	2.044	
Ha	6	25-28	26.0	1.10	0.894	
Ga	18	23-28	25.4	1.54	0.726	
Aa	38	22-29	25.3	1.57	0.510	
Ia	14	22-28	24.7	1.54	0.824	
Dp	9	23-26	24.3	0.87	0.577	
Fp	11	22-27	24.3	1.56	0.934	
Ep	12	21-28	23.6	1.88	1.086	
Ap	31	18-23	21.1	1.29	0.463	
Bp	29	18-27	21.0	1.82	0.677	
Cp	16	18-22	19.9	1.29	0.645	
Em	17	21-27	24.6	1.54	0.746	
Dm	20	21-26	23.5	1.36	0.607	
Cm	52	21-27	23.0	1.72	0.477	
Gm	31	21-25	22.4	1.38	0.497	
Fm	21	19-24	21.5	1.54	0.671	
Bm	54	19-24	21.3	1.27	0.347	
Am	23	19-24	21.0	1.00	0.417	
Hm	8	19-22	20.5	1.31	0.926	
Dc	20	19-26	22.0	1.70	0.761	
Ec	20	19-24	21.4	1.63	0.729	
Ac	7	20-23	21.3	1.25	0.948	
Bc	23	18-23	20.8	1.24	0.518	
Cc	21	19-24	20.6	1.28	0.558	
An	26	17-23	19.1	1.32	0.519	

TABLE 18. Number of Scales Along Forelimb (SAF).

SAMPLE	N	RANGE	$\bar{X}$	SD	$2SE_{\bar{X}}$	STP
Ca	19	25-28	27.1	0.91	0.418	
Fa	30	25-29	26.8	1.01	0.367	
Da	11	25-27	26.2	0.60	0.364	
Ea	16	24-27	25.7	1.25	0.625	
Ia	14	24-27	25.6	0.74	0.398	
Aa	38	22-28	25.3	1.11	0.359	
Ba	6	24-26	25.2	0.98	0.803	
Ha	6	23-25	24.2	0.75	0.615	
Ga	18	22-25	24.0	1.03	0.485	
Dp	9	23-26	24.1	1.05	0.703	
Bp	29	21-25	22.6	1.05	0.195	
Ep	12	21-25	22.6	1.08	0.626	
Cp	16	20-24	22.5	1.15	0.577	
Ap	31	20-24	21.5	1.03	0.369	
Fp	11	20-23	21.3	0.90	0.545	
Em	17	23-26	24.6	1.06	0.516	
Dm	20	23-25	23.8	0.83	0.373	
Gm	31	21-26	23.4	1.02	0.366	
Cm	52	20-27	23.2	1.30	0.362	
Fm	21	21-25	22.9	0.89	0.388	
Am	23	21-23	22.5	0.67	0.277	
Hm	8	21-23	22.1	0.64	0.453	
Bm	54	18-24	21.8	1.19	0.323	
Ec	20	20-25	23.1	1.29	0.579	
Dc	20	20-23	21.7	1.08	0.483	
Bc	23	19-23	21.1	1.08	0.451	
Cc	21	18-22	20.1	1.00	0.434	
Ac	7	19-21	19.6	0.98	0.738	
An	26	20-25	22.4	1.24	0.485	

TABLE 19. Number of Scales Along Third Finger (SF3).

SAMPLE	N	RANGE	$\bar{X}$	SD	$2SE_{\bar{X}}$	STP
Ca	19	10-12	10.8	0.69	0.316	
Fa	30	10-11	10.6	0.49	0.179	
Da	11	9-11	10.1	0.54	0.325	
Aa	38	9-11	10.1	0.63	0.205	
Ia	14	9-11	10.0	0.55	0.296	
Ba	6	9-11	10.0	0.63	0.516	
Ea	16	9-11	9.9	0.68	0.340	
Ha	6	9-10	9.8	0.41	0.333	
Ga	18	9-10	9.8	0.43	0.202	
Dp	9	8-11	9.8	0.97	0.648	
Ep	12	8-9	8.3	0.45	0.261	
Ap	31	8-9	8.2	0.40	0.144	
Bp	29	8-10	8.1	0.44	0.164	
Cp	16	8-9	8.1	0.25	0.125	
Fp	11	8	8.0	0	0	
Em	17	8-10	9.2	0.73	0.353	
Dm	20	8-10	8.8	0.83	0.373	
Gm	31	8-10	8.7	0.75	0.269	
Hm	8	8-9	8.6	0.52	0.366	
Cm	52	8-10	8.5	0.75	0.209	
Fm	21	8-10	8.4	0.67	0.292	
Am	23	8-9	8.3	0.49	0.203	
Bm	54	7-10	8.3	0.63	0.171	
Ec	20	8-10	8.5	0.60	0.270	
Dc	20	8-9	8.2	0.37	0.164	
Ac	7	8-9	8.1	0.38	0.286	
Bc	23	7-9	8.0	0.43	0.178	
Cc	21	7-9	8.0	0.38	0.168	
An	26	8-10	8.1	0.43	0.169	

TABLE 20. Number of Scales Along Fifth Finger (SF5).

SAMPLE	N	RANGE	$\bar{X}$	SD	$2SE_{\bar{X}}$	STP
Ca	19	6-8	7.1	0.40	0.186	
Fa	30	6-8	7.0	0.53	0.192	
Ia	14	6-7	6.9	0.36	0.194	
Da	11	6-7	6.8	0.40	0.244	
Aa	38	6-7	6.8	0.43	0.140	
Ha	6	6-7	6.7	0.52	0.422	
Ea	16	6-8	6.6	0.63	0.315	
Ba	6	6-7	6.5	0.55	0.447	
Ga	18	5-7	6.4	0.70	0.332	
Dp	9	6-7	6.7	0.50	0.333	
Cp	16	6	6.0	0	0	
Bp	29	6	6.0	0	0	
Ep	12	5-6	5.9	0.29	0.167	
Ap	31	5-7	5.9	0.40	0.142	
Fp	11	5-6	5.5	0.52	0.315	
Hm	8	6-7	6.4	0.52	0.366	
Em	17	6-7	6.4	0.49	0.239	
Gm	31	5-8	6.2	0.69	0.247	
Dm	20	6-7	6.2	0.37	0.164	
Cm	52	5-7	6.1	0.40	0.110	
Fm	21	6-7	6.1	0.30	0.131	
Am	23	6-7	6.0	0.21	0.870	
Bm	54	5-7	6.0	0.39	0.105	
Ec	20	5-7	6.3	0.57	0.255	
Ac	7	5-6	5.9	0.38	0.286	
Dc	20	5-7	5.9	0.59	0.263	
Bc	23	5-6	5.7	0.49	0.203	
Cc	21	5-6	5.5	0.51	0.223	
An	26	5-7	6.0	0.28	0.111	

TABLE 21. Number of Scales Along Third Toe (ST3).

SAMPLE	N	RANGE	$\bar{X}$	SD	$2SE_{\bar{X}}$	STP
Ca	19	11-14	12.3	0.73	0.337	
Fa	30	10-13	11.9	0.82	0.299	
Ba	6	11-13	11.8	0.75	0.615	
Da	11	11-13	11.7	0.79	0.474	
Ha	6	11-12	11.7	0.52	0.422	
Ia	14	10-12	11.5	0.65	0.348	
Ea	16	11-12	11.5	0.52	0.258	
Aa	38	11-13	11.4	0.55	0.178	
Ga	18	10-12	11.1	0.47	0.222	
Dp	9	10-11	10.6	0.53	0.351	
Ep	12	9-12	10.3	0.75	0.435	
Ap	31	9-12	10.2	0.62	0.222	
Cp	16	9-12	10.1	0.96	0.479	
Bp	29	9-12	10.0	0.78	0.289	
Fp	11	8-10	9.5	0.69	0.415	
Em	17	10-13	10.8	0.81	0.392	
Dm	20	10-12	10.6	0.69	0.307	
Cm	52	9-13	10.4	0.80	0.221	
Gm	31	9-12	10.3	0.64	0.231	
Hm	8	9-11	10.0	0.53	0.378	
Am	23	9-12	10.0	0.77	0.320	
Bm	54	8-11	10.0	0.71	0.193	
Fm	21	9-11	9.9	0.62	0.273	
Ec	20	8-11	9.7	0.92	0.413	
Dc	20	8-11	9.3	0.92	0.413	
Bc	23	8-10	9.0	0.74	0.308	
Ac	7	8-9	8.7	0.49	0.369	
Cc	21	8-10	8.7	0.80	0.347	
An	26	8-12	10.0	0.77	0.303	

TABLE 22. Number of Scales Along Fourth Toe (ST4).

SAMPLE	N	RANGE	$\bar{X}$	SD	$2SE_{\bar{X}}$	STP
Ca	19	14-17	15.4	0.90	0.414	
Fa	30	13-17	15.2	0.97	0.355	
Ha	6	14-16	15.0	0.89	0.730	
Ba	6	13-16	14.8	0.98	0.803	
Da	11	14-15	14.8	0.40	0.809	
Ea	16	14-17	14.8	0.83	0.417	
Aa	38	13-17	14.7	0.98	0.319	
Ga	18	14-15	14.1	0.32	0.152	
Ia	14	12-15	13.9	0.77	0.412	
Dp	9	12-15	13.6	0.88	0.588	
Ep	12	12-14	12.7	0.89	0.512	
Ap	31	11-15	12.6	0.84	0.301	
Bp	29	11-14	12.5	0.74	0.274	
Cp	16	11-15	12.4	1.15	0.576	
Fp	11	10-13	11.9	0.70	0.423	
Em	17	12-15	13.2	0.97	0.471	
Cm	52	11-16	13.0	1.06	0.293	
Dm	20	12-14	13.0	0.73	0.324	
Gm	31	11-15	12.9	0.91	0.326	
Am	23	11-15	12.5	1.12	0.468	
Hm	8	12-14	12.5	0.76	0.535	
Bm	54	10-14	12.4	0.88	0.240	
Fm	21	11-14	12.2	0.62	0.273	
Ec	20	11-14	12.4	1.05	0.468	
Dc	20	11-13	11.9	0.72	0.321	
Bc	23	10-13	11.3	0.83	0.347	
Cc	21	10-12	11.3	0.58	0.252	
Ac	7	9-11	10.6	0.79	0.595	
An	26	11-15	12.2	0.85	0.333	

TABLE 23. Number of Scales Along Fifth Toe (ST5).

SAMPLE	N	RANGE	$\bar{X}$	SD	$2SE_{\bar{X}}$	STP
Ca	19	10-13	11.1	1.05	0.481	
Ba	6	10-12	10.6	0.82	0.666	
Fa	30	9-12	10.6	0.63	0.229	
Aa	38	8-12	10.4	0.79	0.256	
Da	11	9-11	10.2	0.75	0.453	
Ea	16	9-11	10.1	0.72	0.359	
Ia	14	9-10	9.6	0.50	0.266	
Ga	18	8-10	9.4	0.78	0.369	
Ha	6	9-10	9.3	0.52	0.422	
Ep	12	8-10	9.3	0.62	0.359	
Dp	9	8-10	9.2	0.67	0.444	
Ap	31	8-10	9.2	0.79	0.285	
Bp	29	8-10	8.7	0.75	0.279	
Cp	16	8-10	8.5	0.73	0.364	
Fp	11	8-9	8.2	0.40	0.244	
Em	17	9-10	9.8	0.39	0.191	
Hm	8	9-10	9.6	0.52	0.366	
Gm	31	8-12	9.5	0.81	0.291	
Cm	52	8-11	9.5	0.78	0.216	
Dm	20	8-10	9.2	0.59	0.263	
Am	23	8-10	9.0	0.88	0.366	
Bm	54	8-10	8.8	0.70	0.191	
Fm	21	8-10	8.8	0.70	0.306	
Ec	20	8-11	8.8	0.77	0.343	
Dc	20	7-10	8.3	0.64	0.286	
Cc	21	7-11	8.1	0.73	0.317	
Bc	23	7-9	8.0	0.52	0.218	
Ac	7	7-8	7.9	0.38	0.286	
An	26	7-10	8.3	0.68	0.266	

APPENDIX B

SPECIMENS EXAMINED

Pholidobolus affinis

ECUADOR : *Chimborazo:* 8.4 km N Cubijies, KU 140923-926; 4.1 km E San Juan, 3220 m, KU 140927-28; 10 km N Riobamba, 2730 m, KU 134863; 15 km E Riobamba, 2600 m, KU 121155-60; 8 km SE Licto, 3000 m, KU 140929; Guamote, 3050 m, KU 134859-60; 0.3 km S Tixán, 2885 m, KU 140930-932; 1.1 km S Tixán, 2885 m, KU 140933-34; 2.3 km S Tixán, 2900 m, KU 140935-37; 2.9 km S Tixán, 2905 m, KU 140938-39; 3.3 km S Tixán, 2885 m, KU 140940-42; 10 km NE Alausí, near Tixán, UMMZ 123317. *Cotopaxi:* 0.3 km N Mulaló, 3005 m, KU 140883; 1 km NE Mulaló, 3050 m, KU 127129-30; 2.9 km E Pan American Hwy on road to Mulaló, 2980 m, KU 140884-922; 6 km S, 7 km E Latacunga, 2750 m, KU 127131. *Loja:* Saraguro, 2500 m, KU 134862. *Pichincha:* No specific locality (province probably in error), ZSM 644/0. *Tungurahua:* Ambato, 2700 m, KU 121161-75, UMMZ 90779(4); Río Patate, 2-3 km S Los Andes, USNM 193604-09, 6001-05; Baños, UMMZ 84111-13, FMNH 27671-73, 28036, 28044-45, 28048, USNM 193599-603, KU 140964-65; Cerro Llanganate, USNM 193610-13; 3 km SSW San Miguelito, 2620 m, KU 136411-16; 10 km E Ambato, 2560 m, KU 134861; Chambo Grande, 17.8 km W Baños, 2345 m, KU 140943-49, 140951-63, 142775-785; 4.4 km S Patate, 2070 m, KU 140966; 8.9 km SSE Patate, 2480 m, KU 140967, 140969-84; 13 km SSE Patate, 2750 m, KU 141597, 141601.

Pholidobolus annectens

ECUADOR: *Loja:* Loja, 2150 m, KU 121179-80, 135219-20; 2 km E Loja, 2200 m, KU 121181-97; 3 km W Loja, 2150 m, KU 135216-18; 4.9 km E Loja, 2335 m, KU 140985; 4.6 km N Loja, 2065 m, KU 140986-87; 4 km W Loja, 2280 m, KU 140988, 140990-92, 141602-03.

Pholidobolus macbrydei

ECUADOR: *Azuay:* Contrayerbas, W of Cuenca, AMNH 23446; Laguna de Zurucuchu, 28 km SW Cuenca, 3200 m, KU 121256-58, CAS 94110; 3.9 km S Cutchil, 2855 m, KU 141028; 10.5 km S Cumbe, KU 141029; 21.6 km S Cumbe, 3310 m, KU 142791; 4.4 km NE Girón, 2315 m, KU 140606. *Cañar:* 24 km N Cañar, 3962.4 m, AMNH 24345; 8 km NW Biblián, 3420 m, KU 136417; E slope Cerro Bueran, 3685 m, KU 141041-44; 14.2 km N Biblián, 3430 m, KU 140994-141014, CAS 132581, USNM 193217; 9.1 km N, 2.3 km W Biblián, 3070 m, KU 141015-141027, 141605-09, 140993, CAS 132582; 9.1 km N, 3.3 km W Biblián, 3015 m, USNM 193218; 15 km SSE Cañar, on road to Azogues, UMMZ 123318-19. *Chimborazo:* 10 km W San Juan, 3400 m, KU 121259-62; 12 km SW Cajabamba, 3800 m, KU 121263-69; Urbina, 3609 m, UMMZ 123316. *Loja:* 11 km NE Urdaneta, 2970 m, KU 142789-790; 6 km N San Lucas, 2850 m, KU 121246; 9.5 km S Saraguro, 3120 m, KU 141045-47, 141604; 13.2 km E Loja, 2770 m, KU 141048. *Morona Santiago:* 8 km S Cutchil, 3040 m, KU 121249-55, 121275; 12 km S Cutchil, 3400 m, KU 121247-48; 9.6 km S Cutchil, 2935 m, KU 141030; 11.5 km S Cutchil, 2820 m, KU 141031-39. *Tungurahua:* 10 km W Cotaló, 3300 m, KU 136418-19. *Zamora-Chinchipe:* 13-14 km E Loja, 2850 m, KU 121242-45; 15 km E Loja, 2800 m, KU 121235-41; 13.9 km E Loja, 2775 m, KU 141051; 14 km E Loja, 2775 m, KU 141052-53; 13.8 km E Loja, 2780 m, KU 141049; 13.5 km E Loja, 2800 m, KU 142786-788. *Province Unknown:* western Ecuador, ZMB 900.

Pholidobolus montium

ECUADOR: *Cotopaxi:* 32 km S Aloag Junction, 3000 m, KU 141086-87; 0.3 km W Mulaló, KU 141088; 2.9 km E Pan American Hwy on road to Mulaló, 2980 m, KU 141089-92, 141610-13. *Imbabura:* Ibarra, 2000 m, UIMNH 91538-559, UMMZ 51282; Lago Cuicocha, KU 142874-93; 1 km N Otavalo, 2560 m, KU 118070-100, 129182-84, MCZ 101874-81; near Otavalo, UMMZ 105907; Otavalo, 2550 m, UMMZ 105908-10, KU 134956-64. *Pichincha:* Cayambe, 2800 m, UMMZ 105911-(8), UIMNH 91483-524; 0.5 km N Cayambe, 2820 m, KU 136420-27; 4 km W San Antonio, 2550 m, KU 134885-904; San Antonio, 2500 m, KU 134939-955; 10 km S Cayambe, MCZ 80973; Quito, 2840 m, AMNH 28771-82, KU 94529, 112220-21, RMNH 3401; Valle de los Chillos, 2.5 km E Río Chiche, KU 141055-141085, 141261, 141614-17; 14 km W Chillogallo, 3190 m, KU 142795; Lloa, UMMZ 55526; Cerro Pichincha, E slope, 2900 m, KU 112224-26; 5 km W Aloag, 2945 m, KU 109816; 16 km E Aloag, 2810 m, KU 112222-23; Machachi, CAS 39520, MCZ 8410-11. *Tungurahua:* Baños, Río Pastaza, AMNH 60611-14.

Pholidobolus prefrontalis

ECUADOR: *Azuay:* 4 km E Cuenca, 2540 m, KU 134864-68; 6 km N Cuenca, AMNH 91827-32; Cutchil, 3.6 km S Sigsig, 2530-5 m,

KU 141125-135, 141619-20; above Gualaceo, 2295 m, KU 141136; 8.7 km N Cuenca, KU 141137; 8.8 km NW Cuenca, 2620 m, KU 141138. *Bolivar:* Guaranda, 2640 m, KU 134907-38; San José del Chimbo, 2450 m, KU 134905-06; 8.6 km S Guaranda, 2500 m, KU 142792-3. *Cañar:* Biblián, 2615-20 m, KU 141123-24, 142794; 0.5 km S Río Cañar on Pan American Hwy, 2835 m, KU 141114-22. *Chimborazo:* Alausí, 2400 m, KU 134869-84; 3.3 km S Tixán, 2885 m, KU 141094-99, CAS 132584, KU 141100; 4 km S Tixán, 2820 m, KU 141101; 4.9 km S Tixán, 2785 m, KU 141102-04, CAS 132583, USNM 193220; 3.3-4.9 km S Tixán, KU 141093, 141105-141113, 141618, 141621-23, USNM 193219.

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